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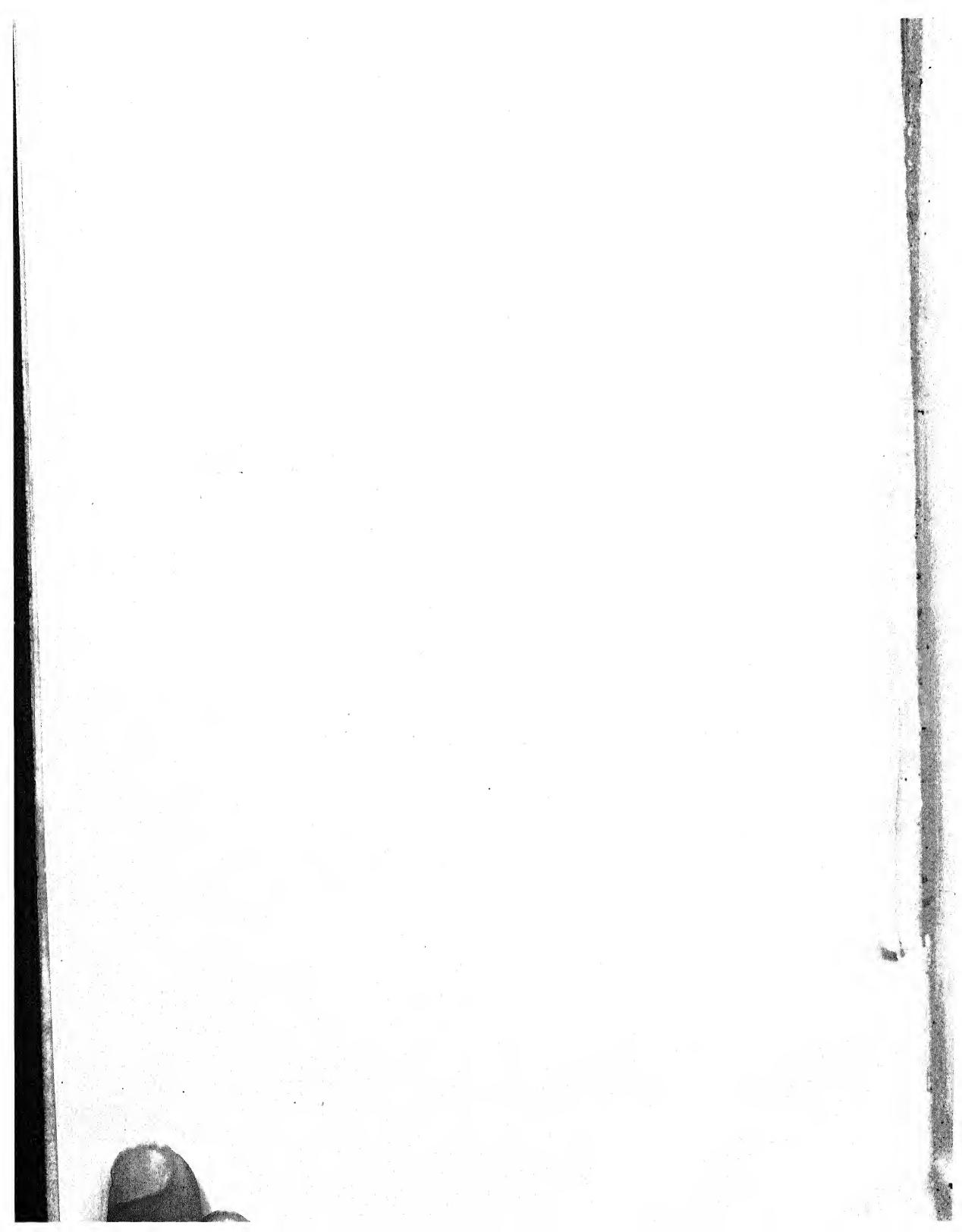
STUDIES ON THE VEGETATION OF ICELAND

BY

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WITH 12 PLATES

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PREFACE.

A mong the results achieved by Danish botanical research, two especially aroused my liveliest interest, viz. W. Johannsen's demonstration of the fixity of the genotype ("the genotype of homozygotic organisms is normally just as "fixed in type" as e. g. chemical composition" (Arvelighed 1918, p. 102)), and C. Raunkiær's demonstration of the distribution of the life-forms within the various climatic zones ("even the most widely separated regions with entirely different floras in a floristic respect but with essentially the same climatic conditions for plant life show in the main the same biological spectrum" (Livesformerne Statistik som Grundlag for biologisk Plantogeografi. 1908, pp. 68—69).

From these two facts I, as an impartial observer, drew the conclusion that in Nature the development of forms as sketched in "Livesform og Alder" (Bot. Tidsskr. 40: 193—203, 1928) must in the last instance be regarded as a physico-chemical process, the simplest manifestation of which is to be found in the transformation of a chemical combination, such as e. g. that of H_2O from vapour through water to ice (the gaseous, liquid, and solid phases respectively) during progressively decreasing temperature. In this way the species should be chemical combinations whose phases are their life forms.

This, however, is merely a theory, the correctness of which is primarily determined by its fruitfulness as a scientific working hypothesis. Hence it was expedient to collect further material to illustrate the relation between form and environment. As assistant to Professor Raunkiær in his investigation of the preserved heath at Nørholm (in the summers of 1921—1924) I was fortunate enough to become acquainted with the zone formation around collections of water, to which the attention of botanists had already been drawn in "Vesterhavets Øst- og Sydkysts Vegetation" (Raunkiær 1889). At Nørholm Heath I was able to collect material to elucidate the amount of individual species and life-forms in the various zones of moisture, and thanks to financial

aid from the "Japetus Steenstrup Legat" I could continue and verify my observations from Nørholm Heath in the summer of 1924 by a journey through the dune region along the west coast of Jutland.

When I had taken my Master's degree in the autumn of 1924, thanks to testimonials from my teachers Professors C. Raunkiaer, L. Kolderup Rosenvinge and C. H. Ostenfeld, I obtained financial aid from the Carlsberg Foundation and from Dansk-Islandske Forbunds-fond for phytogeographical researches in Iceland.

In this work, too, luck befriended me. While making my preparations for the journey to Iceland, I was able to attend a course of lectures on the vegetation of Greenland given at the University in the spring term of 1925 by Professor Ostenfeld. These lectures have been of the greatest importance to me, partly during my work in Iceland, and partly during the subsequent more thorough treatment of the material. Thus it is to them I owe the impulse to include in my investigations the vegetation under the various depths of snow-covering, my original intention being only to investigate the vegetation in the various zones of moisture. Also the division of the Icelandic flora into species-groups according to the geographical distribution of the species, the setting up of species group spectra on a parallel with the biological spectra, and the application of the species group spectra for a more thorough characterisation of the environment, are fruits of these lectures. By these investigations the conception of the species as chemical combinations has been further confirmed.

I have regarded the financial aid which rendered possible the researches described in this treatise as a great mark of confidence and, to the best of my ability, I have endeavoured not to disappoint the trust placed in me. Through this work I beg the Trustees of the Carlsberg Foundation and the Trustees of the Dansk-Islandske Forbunds-fond to accept my respectful thanks. Finally I owe thanks to Miss Annie I. Fausbøll, M. A., who has undertaken the difficult task of the English translation.

Copenhagen, June 1928.

I. THE ICELANDIC CLIMATE.

THE climate of Iceland is, according to Thoroddsen 1914 p. 265 f., determined not only by the geographical situation of the island and the prevalent winds of the North Atlantic, but also to a great extent dependent on the current-conditions of the surrounding seas.

The south and west coasts of Iceland are washed by the warm Gulf Stream, while on the north and east coasts we have the cold polar current. The waters of the two currents meet in the sea outside south-east of Iceland itself, on a line running from Vatnajökull to the Færöes and to the north-west off Cape Horn. It is as well to note at once that in the highland tracts of Iceland between these two points, we find a series of jökulls in decreasing volume from Vatnajökull to the jökulls of Vestfirðir.

The current conditions may be more precisely described as follows: The Gulf Stream washes the shores of Iceland all along the south and south-west coasts of the island, gradually gathering to a stream which follows the coast towards the west and further towards the north. Off Cape Horn, this branch of the Gulf Stream, known as the Irminger Current, encounters the Polar Current coming from the Polar Sea. A branch of the Irminger Current again is forced outward from the coast by this Polar Current, and another branch, rounding Cape Horn, follows the northern coasts of the island to the eastward, cooling as it goes, and finally disappearing under the water masses of the Polar Current itself. At Grímsey, it is still of great importance, but farther east, it vanishes altogether, and the shores of East Iceland are thus washed solely by the polar water. The situation, then, is as follows: the south and west coasts, i. e. the coast south of the "jökullslíne" is washed exclusively by water from the Gulf Stream. The north and east coasts are washed by polar water; the eastern by this alone, the northern by this and Gulf Stream water as well.

According to Thoroddsson (1914) these features are of great importance in their bearing on life in the sea, both as regards its flora and fauna. We find, in fact, on the north and east coast, a flora and fauna of arctic character, whereas those of the south and west coasts are of temperate character. Up to the present, this has been confirmed by investigations on the flora of marine algae, plankton, and the fish fauna, as well as deep sea and bottom fauna. The same conditions seem to be of no slight importance as regards life on land, as the present research *inter alia* will show.

The temperature along the coast shows, according to Thoroddsson, the following values: On the south and west, the mean surface temperature is 5—7° C., while to the north and east it is somewhat lower, 3—4° C.

At the Vestmannaeyjar (South Iceland) the surface water during the coldest months (Decbr.—Febr.) shows a monthly average of abt. 4° C., and in the hottest months (July—Aug.) abt. 11° C., the annual mean temperature being abt. 7° C.

Stykkishólmur (W. Icel.) has for Febr.—March temperatures of 0.3°—0.4° C. and July—Aug. 10.4°—10.6° C., with an annual mean temperature of 4.9° C. Grímsey (N. Icel.) a March temperature of 0.7° C., August 7.4° C., with an annual mean of 3.8° C., and Papey (E. Icel.) has a Febr.—March temperature of 0.4°—0.5° C., Aug.—Sept. 6.6°—6.2° C. with a mean temperature for the year of 3.2° C.

It will be seen from this that the temperature of the surface water decreases parallel with the volume of Gulf Stream water. From South Iceland west and northward round to East Iceland we have the following values for mean annual temperature: 6.9°—4.9°—3.8—3.2° C. East Iceland has the lowest mean temperature and the greatest volume of the Polar water; South Iceland the greatest volume of Gulf Stream water and the highest mean annual temperature.

The temperature of the air is closely correlated to this (see Table 1), being, however, nearly always lower than the surface temperature of the sea water, the difference amounting on the average to a couple of degrees. We find, for instance for the temperature of the air, the following mean values: 5.1°—3.0°—1.5°—2.4° C. that is, following the coastline round from S-W-N-E.

The greatest difference is apparent during the coldest months of the year, October to March, less in summer from April—Sep-

tember, and we find also, that only on the south and west coasts is the temperature of the air, on the average, always lower than that of the sea water, whereas on both north and east the temperature of the air may remain for months higher than that of the sea water, this being especially the case on the east coast.

The Polar Current carries with it great masses of ice. This current of ice can either strike Langanes or the east coast of Vestfirðir, south of Cape Horn. If it strikes Vestfirðir, then it is borne by the eastward going current along the north coast, rounding Langanes and drifting on along the east, sometimes even also along the south coast, until all the ice has melted or disappeared out into the Atlantic. When the current of ice strikes Langanes or Melrakka-sljetta, it is carried out into the Atlantic by the same current. The quantity of drift ice varies to an extraordinary degree; in some years there may be none at all, while in others, "ice years", it may lie about until far on in summer. The result is seen in great climatic fluctuations.

The winds in Iceland are determined by two centres of low barometric pressure, one lying south-west of Iceland, and another, minor one, situated towards the north-east. The former constitutes the principal factor in determining the state of the wind, and in consequence, easterly winds are most prevalent, especially on the west. In East Iceland, the eastern minimum is of no slight importance, westerly winds being here of more frequent occurrence than in other parts of the country.

The highest frequency percentage for calm occurs in summer, and this applies to all parts of the country; the highest percentage is recorded from the Vestmannaeyjar, with an average value of 22, a percentage of calm in winter of 10—20 and in summer of 25—30. At Grimsey the percentage of calm is lowest, on an average about 10, 4—6 in winter, 16—19 in summer. East and West Iceland show somewhat similar conditions, though in winter the percentage is higher, about 10.

The number of stormy days is closely correlated to this (see table 1). It applies to all parts of the country that the number is highest in winter, lowest in summer. It is, however, very variable. It storms most frequently in the south-west and south. Thus Stykkishólmur has, on an average, 50 stormy days per annum, the Vestmannaeyjar 25. The number is considerably less for the north and east. Grímsey has 11, Berufjörður only 8 stormy days annually.

These facts, however, seem merely to apply to conditions either at the level of the sea, or perhaps only by the coast. If we take a station like Möðrudalur, situated approximately on a line connecting Grímsey with Berufjörður, but at an altitude of 480 m above sea level, this station shows an average of 39 stormy days annually, though distributed in such a way that the winter has the highest, the summer the lowest number of stormy days.

Temperature conditions. Above we saw that the temperature of the air near the sea was very closely correlated to the surface temperature of the sea water, but with the addition that the temperature of the sea water was always higher, 1—2° C., than that of the air. In table 1 are shown the average annual and monthly mean temperatures for South Iceland, West Iceland, East Iceland, and the highland Möðrudalur. There is a considerable difference between the coastal stations on the one hand and the highland on the other hand, a difference which may also be shown to exist between the coastal stations mutually.

The mean temperature is highest in South Iceland, being 5.1° C. at the Vestmannaeyjar. The coldest month here is December with a mean temperature of 1.2°, the warmest month is July with 10.6°. The difference between the coldest and warmest months is 9.4°. West Iceland, Stykkishólmur, has a mean annual temperature of 2.8°, the coldest month, February, registering a mean temperature of 2.7° below zero, the warmest month (July) 9.7°, with a difference of 12.4°.

Berufjörður in the east country has the same mean annual temperature, 2.3°; here March is the coldest month, 1.7° below zero, July the warmest, 8.5°, and the difference between the coldest and warmest months is somewhat less, 10.2°.

Grímsey, in the north country, has a mean annual temperature of 1.5°, a mean temperature for March of 3.6° below zero, for July of 7.0°, difference 10.6°.

The highland is considerably colder. The mean annual temperature for Möðrudalur is 0.2° below zero, the January temperature, 7.2° below zero, the July temperature 10.0°. The difference, 17.2°, is thus considerably greater than that of the coastal stations.

The number of frosty days is closely correlated to the temperature conditions. The smallest number is recorded from South Iceland which shows an average of 109 per annum. Grímsey has the greatest number, 192. Berufjörður lies between these two extremes with 158 frosty days and Stykkishólmur with 166 frosty days. Un-

fortunately there are no records from the highlands. The number is probably considerably higher here.

Precipitation. The precipitation in summer is principally rain, in winter principally snow. The annual precipitation is greatest to the south and east, decreasing towards the west and being comparatively small in the north.

In the Vestmannaeyjar the annual precipitation is 1319 mm. (see table 1), distributed over 207 days, in East Iceland it is 1117 mm., distributed over 146 days, in West Iceland, Stykkishólmur, the amount of precipitation is already considerably lower, 662 mm. distributed over 117 days. From the highland tracts we have unfortunately no investigations on the amount of precipitation for the whole year, so it is impossible to draw any comparison with the coastal stations. The number of days with precipitation for Möðrudalur is 153, thus somewhat higher than for Grímsey, corresponding fairly well with East Iceland. It may, however, be taken for granted that the amount of precipitation is not nearly as great in the highland tracts as at the coast. Observations from some of the summer months at a highland station, Grímsstaðir, about 385 m above the sea, in the vicinity of Möðrudalur, show an average monthly value for the five months May—September of 26.8 mm, while the average monthly amount of precipitation for Grímsey for the five months is 31.4 mm.

The amount of precipitation and the number of days with precipitation are highest in the autumn and winter months, lowest in spring and summer. This applies especially to the regions to the south of glaciers.

In winter the precipitation occurs principally in the form of snow, though with a difference in the different parts of the country. Table 1 shows the number of days with snow for the different stations where this has been investigated. In the highland tracts and the north country snow predominates, in the south there are comparatively few days with snow; while snow is rare here in the summer, it is more frequent in the north. In the highland tracts snow in summer is even the rule. At Möðrudalur the average monthly number of days with snow in summer is 2—4.

Unfortunately there are no observations on the depth and duration of the snow-covering in the various regions of Iceland. As to the depth of the snow-covering Thoroddsen states that it varies much with the situation and the altitude above the sea, and from one year to another. As to its duration he states that the snow

TABLE 1.

Climatic Conditions in Iceland.

- I. Berufjörður, East Iceland ($64^{\circ} 40' N.$, $14^{\circ} 15' W.$, 18 m above sea level).
- II. The Vestmannaeyjar, South Iceland ($63^{\circ} 26' N.$, $20^{\circ} 18' W.$, 8 m above sea level).
- III. Stykkishólmur, West Iceland ($65^{\circ} 5' N.$, $22^{\circ} 46' W.$, 11 m above sea level).
- IV. Grímsey, North Iceland ($66^{\circ} 34' N.$, $18^{\circ} 3' W.$, 2.5 m about sea level).
- V. Möðrudalur, Highland Tracts ($65^{\circ} 19' N.$, $15^{\circ} 15' W.$, about 480 m above sea level).

The table has been compiled after Thoroddsson (the lowland stations), Thorkelsson (the precipitation values for all stations), and Meteorologisk Aarbog Part II, 1886—1916 (the highland station). The lowland stations comprise the years 1872—1906, the precipitation values cover an additional number of years.

	Year	January	February	March	April	May	June	July	August	September	October	November	December
I. Mean temperature of surface water in degrees C°.....	3.2	0.7	0.4	0.5	1.5	3.1	4.8	6.0	6.6	6.2	4.3	2.6	1.3
Mean temperature of air	2.8	-1.2	-1.5	-1.7	1.0	3.7	6.8	8.5	8.3	6.6	3.3	1.1	-1.0
Mean precipitation in mm	1174	128	99	77	83	73	67	64	82	126	124	113	139
Number of days with precipitation	146	15	14	12	11	10	9	10	10	13	13	14	15
Number of days with snow	50	8	8	9	5	3	0.4	»	0.1	0.5	3	6	7
Number of days with fog	171	11	11	11	14	17	19	21	18	16	12	11	10
Number of days with frost	158	24	22	25	18	10	2	»	0.3	2	13	18	24
Number of days with gales	8	1	1	1	1	0.4	0.1	0.2	0.2	0.4	1	1	1
II. Mean temperature of surface water in degrees C°	6.9	4.1	4.1	4.5	6.1	7.7	9.5	10.9	10.8	9.1	6.8	5.1	4.1
Mean temperature of air	5.1	1.3	1.3	1.4	4.0	6.3	9.0	10.6	10.2	8.2	5.1	3.0	1.2
Mean precipitation in mm	1354	150	123	118	94	80	80	77	76	139	144	135	138
Number of days with precipitation	207	21	18	17	17	15	15	15	14	18	19	19	19
Number of days with snow	44	9	8	8	4	1	0.2	»	»	0.3	2	4	8
Number of days with fog	49	2	2	2	3	5	8	8	6	5	4	2	2
Number of days with frost	109	20	18	17	10	3	0.1	»	0.4	1	8	13	19
Number of days with gales	25	4	3	3	2	1	0.5	0.3	0.3	2	2	3	4

TABLE 1 CONTINUED.

	Year	January	February	March	April	May	June	July	August	September	October	November	December
III. Mean temperature of surface water in degrees C°	4.9	0.9	0.3	0.4	1.7	4.7	8.2	10.4	10.6	9.1	6.3	3.7	1.8
Mean temperature of air	2.8	÷2.2	÷2.7	÷2.3	0.8	4.3	7.8	9.7	9.2	6.8	3.2	0.5	÷1.3
Mean precipitation in mm	654	74	69	50	37	37	37	34	41	70	77	69	62
Number of days with precipitation	207	21	19	18	16	15	15	14	14	18	18	19	20
Number of days with snow	84	16	14	13	8	3	0.4	0.1	»	1	4	10	14
Number of days with fog	9	0.3	0.5	0.4	0.7	2.0	1.3	1.6	1.3	0.7	0.3	0.4	0.3
Number of days with frost	166	26	25	26	19	9	1	»	0.1	1	13	20	26
Number of days with gales	50	6	6	6	4	4	2	1	2	4	5	5	5
IV. Mean temperature of surface water in degrees C°	3.8	1.8	1.4	0.7	1.3	2.6	4.2	6.6	7.4	6.9	5.3	4.1	2.9
Mean temperature of air	1.5	÷2.0	÷3.0	÷3.6	÷1.2	1.7	5.5	7.0	6.8	5.7	2.5	0.0	÷1.3
Mean precipitation in mm	274	16	17	17	13	15	18	28	34	34	35	29	20
Number of days with precipitation	117	10	10	10	9	8	6	8	10	11	12	12	11
Number of days with snow	64	7	8	8	7	5	2	0.5	0.4	2	6	9	9
Number of days with fog	46	1	1	2	4	6	7	10	8	4	2	0.5	0.3
Number of days with frost	192	25	24	27	24	17	5	2	2	4	17	21	24
Number of days with gales	11	2	1	1	0.3	0.2	0.4	0.2	0.2	1	1	2	2
V. Mean temperature of air	÷0.2	÷7.2	÷6.7	÷6.4	÷2.1	3.2	8.5	10.0	7.4	4.0	÷1.0	÷4.7	÷6.8
Mean precipitation in mm (Grimstaðir)	»	»	»	»	»	19	27	29	34	26	»	»	»
Number of days with precipitation	153	13	13	14	13	12	8	12	15	12	13	13	15
Number of days with snow	109	12	12	13	12	8	3	2	4	7	10	12	14
Number of days with fog	11	1	1	1	1	1	0.3	1	1	1	1	1	1
Number of days with gales	39	6	4	4	2	2	3	1	1	4	3	4	5

often remains on the ground for a long time in the north country, while this is more rarely the case in the south-west. In the south country it may often happen that the lowland tracts are destitute of snow for months on end. Here the precipitation is in the form of rain, whereas, in the adjacent highland tracts it falls as snow.

Fog. In the calm and rainy regions to the east and south, fogs often occur, whereas the more storm-blown west coast is rarely visited by fog. Thus Berufjörður has no less than 171 annual days of fog, while Stykkishólmur has only 9 days of fog. Fog occurs most frequently in summer, still even the winter months show a number of foggy days on the east coast, about 10.

If on the basis of the above statements, we attempt to make a comprehensive survey of the climate of the separate parts, we must distinguish between a lowland climate and a highland climate.

The lowland climate is of a pronounced oceanic character with but slight difference between the summer and winter temperatures. The climate of the east country is cold, foggy, and rainy, with slight circulation of the air. That of the south country is warmer, especially in winter. In the west country, again, the temperature falls somewhat, and the precipitation is considerably less. Fog is rare, but on the other hand, the weather grows very stormy. The north country is the coldest, but on the other hand the driest. Fog and storm are not very common (the station here is Grímsey, which does not, probably, give a perfectly valid picture of the climatic conditions of the north country).

The main difference between the north and south countries is that the north country is more continental in character than the south country. The summer temperature is very much the same for both parts, the average for all stations being about $9-10^{\circ}$ C., but the winter is considerably colder in the north than in the south, 4° C. below zero in the north, 1° C. below zero in the south. The difference between the warmest and the coldest month is 13.2° in the north, but only 11° in the south.

The highland climate. The climate of the highland tracts is considerably more continental than that of the lowlands. The summer temperature is very much the same in both places, but the winter temperature is considerably lower in the highland tracts and

the difference between the coldest and the warmest months is thus great, 17.2° C. The precipitation is slight and storms are frequent. To this must further be added a probably very thick and at any rate constant covering of snow in winter.

Of interest in connection with plant geography is further the situation of the jökulls and the snow-line. We have previously seen that most of the jökulls gather along a line connecting the two places where the waters of the Gulf Stream and the polar water meet, respectively to the south-east and the north-west of Iceland. The line begins with the large Vatnajökull on the south-east and extends north-westwards over Tungnafellsjökull, Hofsjökull, Langjökull, and Eiríksjökull until it terminates in Gláma and Drangajökull in Vestfirðir. To the north of the range of jökulls there are only a few small jökulls on the peninsula between the Eyja- and Skagafjörður while to the south we have the large Mýrdalsjökull and some smaller ones, more especially Snæfellsjökull.

The area of the jökulls is largest towards the cold, humid, and foggy eastern regions and decreases strongly towards the north-west. The area of Vatnajökull is about 8000 km^2 ; of Hofsjökull about 1350 km^2 , of Langjökull 1300 km^2 , of Gláma about 60 km^2 , and of Drangajökull 350 km^2 . Vatnajökull's greatest altitude above sea level is 2119 m., that of Hofsjökull 1700 m., of Langjökull 1400 m., of Gláma and Drangajökull about 900 m.

The snow-line lies at very different altitudes, coming down lowest on the south side, while on the north side it lies somewhat higher, the east and west sides occupying an intermediate position. On Vatnajökull the snow-line on the north side lies at a height of 1300 m., on the north side of Hofsjökull at 1200 m., and on the north side of Langjökull at a height of 1100 m. On the south side the snow-line lies at a level of 900 m. In Vestfirðir the height of the snow-line above the sea is 400—650 m. On Mýrdalsjökull the snow-line lies at a height of 1100 m. on the north side, and 800—900 m. on the south side.

Below the snow-line proper comes a zone with snow-drifts which either never melt, the permanent snow-drifts, or only melt in very hot summers, the variable snow-drifts. It is difficult to set any lower limit to these two zones. On Arnarvatnsheiði north-east of Langjökull, where the snow-line lies at a height

of 1000—1100 m., the lower limit of permanent snow-drifts lies at a height of 600—700 m. above sea level, and that of the variable snow-drifts at a height of 500—600 m.

The setting up of climate zones, i. e. of a zone of lowland climate, a zone of highland climate, and various snow zones, results in a similar formation of floristic and vegetation zones to which we shall contribute in the following.

II. CLIMATE AND FLORA.

THE above-described rather rigorous climate in connection with the homogeneous soil, consisting of basaltic rocks and their weathering products, is no doubt in great part, and perhaps even more than the isolated position of the island, responsible for the paucity of species apparent in the phanerogams. Thus the most recent treatment of the Icelandic flora, St. Stefánsson's "Flóra Íslands", 2. ed. 1924, gives a total of only 375 phanerogams and vascular cryptogams (the number of species of Taraxacum and Hieracium is, however, taken from the 1st edition of the Flora, 1901).

The floristic peculiarities are here disregarded. They have previously been treated by Grønlund and Warming. Some biological facts are of greater interest in this connection.

In »Flóra Íslands« the country is divided into 5 areas, viz. the East Country or the land between the Langanes Mountains and Hornafjörður; the North Country between the Langanes Mountains and Hrútafjörður; the North West Country or Vestfirðir; the South West Country between Gilsfjörður and the Reykjanes Mountains, and finally the South Country between the Reykjanes Mountains and Hornafjörður. The distribution of each species in each of the aforementioned 5 areas is given in the Flora. By determining the life form of each species and calculating the percentage of the various life forms in the total number of phanerogams we arrive at the biological spectra given in table 3, p. 17, partly for the whole country partly for each of the 5 areas. Of greatest interest are the chamaephytes, the chamaephyte percentage for the whole country being 15.2; hence, as shown by Raunkiær in 1908, Iceland belongs to the subarctic hemicryptophyte-chamaephyte area. For the rest there is a striking, even though slight, difference in the content of chamaephytes in each of the 5 areas. The South Country has a chamaephyte percentage of 15.1, the South West Country has 15.2,

Vestfirðir 16.0, the North Country 16.6, and the East Country 18.0. There is thus an unbroken rise in the chamaephyte percentage from the South Country, whose chamaephyte percentage corresponds to that of the whole country, towards the west and north, until it attains its highest value, 18.0, in the east. It is difficult to ascertain what climatic factor causes this rise, and more probably we may assume that not one but many factors are determining. The physical factor which varies parallelly with the variations in life forms is the annual mean temperature of the oceanic surface water. This as we showed above, was closely correlated to the amount of Gulf Stream water and Polar water at the coasts. The variation in other climatic conditions, whether it be in the air temperature, number of days with frost, the coldest or warmest month, amount of precipitation, number of days with precipitation, days with snow, frost or gales, does not agree nearly so well with the variation in life form as the temperature conditions of the surface water.

The correlation of the biological peculiarities of the flora, more especially of the chamaephyte percentage, and the current conditions of the adjacent seas is likewise confirmed in the surrounding countries. Table 2 gives the biological spectra for West and East Greenland, calculated on the basis of the flora lists given by Ostenfeld (1926).

The west and east coasts of Greenland are each divided into 8 minor corresponding areas. The east coast is washed by a Polar current coming from the north, the Greenland Current, while the west coast is washed by a current coming from the south. In accordance herewith we find that the chamaephyte percentage in the individual, corresponding, minor areas as well as for the two coastal tracts as a whole is highest in the east, lowest in the west. The table shows the composition of the biological spectra. Starting from the number of species, the chamaephyte percentage for the whole of East Greenland is 25.2, for West Greenland 21.6. Starting from the points sum, the ratio will be 28.6 to 25.2. Only South Greenland has a chamaephyte percentage lower than 20, viz. 18.6.

If we pass over to the west coast of Baffin Bay and Davis Strait, we find that a current from the north, the Labrador Current, flows along the eastern coast of Baffin Land, and according to Raunkiaer (1908), the chamaephyte percentage for Baffin Land is 30, while for the whole of West Greenland it was only 21.6.

Passing from Iceland towards the east, we find the west coast of Norway washed by the warm Gulf Stream, and here, as a matter

TABLE 2.

The Biological Spectra of West and East Greenland.

	Pt	n	Ph	Ch	H	G	HH	Th ¹⁾
W. Grl. 80°—83° N. Lat. VIII . . .	2.9	69	>	31.9	53.6	10.1	4.3	>
76°—80° — VII . . .	5.5	109	>	31.2	52.3	11.0	4.6	0.9
71°—76° — VI . . .	5.4	149	>	30.2	51.7	12.8	4.0	1.3
69°—71° — Va . . .	5.1	197	>	27.4	52.3	11.8	6.1	2.5
Disko Vb . . .	7.5	214	>	25.7	53.3	12.1	6.1	2.8
66°—69° — IV . . .	6.0	233	>	25.8	51.1	9.9	9.0	4.3
64°—66° — III . . .	7.8	217	0.5	24.4	54.8	9.7	7.4	3.2
61°—64° — II . . .	9.3	216	1.4	21.3	56.5	8.8	7.4	4.6
S. Grl. 61°—60°—61° I . . .	11.4	236	1.3	18.6	54.2	10.6	7.6	7.6
E. Grl. 61°—65° N. Lat. II . . .	9.2	153	>	22.9	60.1	9.2	4.6	3.3
Angmagsalik III . . .	9.0	167	>	24.6	58.1	8.4	6.0	3.0
67°—70° N. Lat. IV . . .	7.5	120	>	30.8	54.2	9.2	4.2	1.7
Scoresby Sound V . . .	6.3	160	>	29.4	52.5	12.5	3.8	1.9
72°—76° N. Lat. VI . . .	4.8	126	>	29.4	54.0	11.9	2.4	2.4
76°—81° — VII . . .	5.5	91	>	33.0	49.5	14.3	3.3	>
81°—83° — VIII . . .	4.3	47	>	42.6	44.7	10.6	2.1	>
West Greenland	8.2	352	0.9	21.6	54.0	10.5	7.7	5.4
East Greenland	7.1	238	>	25.2	57.6	10.0	4.2	2.9
West Greenland	7.3	1640	0.4	25.2	53.4	10.7	6.7	3.6
East Greenland	7.1	864	>	28.6	54.6	10.6	4.1	2.1

of fact, the chamaephyte percentage is considerably lower. According to Raunkiær (1908), Tromsø in 69—70° N. has a chamaephyte percentage of 10, and Vardø, in a still more northerly situation but protected from the sea, has a chamaephyte percentage of c. 15.

It is thus beyond doubt that there is a connection between the biological spectra and the current conditions of the surrounding seas.

For the rest it is probably the temperature conditions which have most influence on the composition on the flora, that is to say, the annual mean temperature or more probably perhaps the temperature conditions of the winter. Passing from the lowlands to the highland, the annual mean temperature, as shown above, grows

¹⁾ In the tables the abbreviations are as follows: n: number of species, Pt: Pteridophytes, Ph: Phanerophytes, Ch: Chamaephytes, H: Hemicyclopediae, G: Geophytes, HH: Helo- and Hydrophytes and Th: Therophytes.

lower and lower, while the winter grows colder and colder. At the same time the flora shows a greater and greater paucity of species. Unfortunately Stefánsson's "Flóra Íslands" gives no upper limit for the individual species, and as far as Iceland is concerned, only very few authors have stated at what altitudes they have found the plants collected by them. Thoroddsen (1914) has given most in this respect. By comparing what is found in the literature concerning the occurrence of the plants in the highland tracts with my own notes, but especially thanks to a long series of flora lists courteously left at my disposal by Mr. Pálmi Hannesson, I have been able to work out the biological spectra of the highland tracts of Iceland given below, divided into zones of 100 m each, from 300 m to 1200 m, the highest locality in which plants have been found.

While 375 species of vascular plants have been found in the whole country, only 224 species have, up to the present, been found above the 300 m curve, and only c. 100 species above the 600 m curve. Going higher still, we find only 40 species above the 800 m curve, and the number is further reduced when we reach the snow-line above which all higher plant life is excluded. It applies to Iceland as to other arctic regions, the Faeroes, northern Norway and Greenland, that only a limited number of species has any lower limit, while most of the species decrease as we go upward and sooner or later reach their upper limit. The following species are of common occurrence right up to the snow-line: — *Luzula arenata*, *Elymus arenarius*, *Poa glauca*, *P. alpina*, *Festuca ovina*, *Salix glauca*, *S. herbacea*, *Oxyria digyna*, *Cerastium alpinum*, *Silene acaulis*, *S. maritima*, *Ranunculus glacialis*, *Arabis petræa*, *A. alpina*, *Empetrum nigrum*, *Saxifraga groenlandica*, *S. oppositifolia*, *S. nivalis*, and *Armeria vulgaris*. With few exceptions all the above-mentioned species are of common occurrence in Greenland right up into the northern parts.

From considerations of space the species lists are not included. The biological spectra calculated from them are given in table 3. There is a difference in the occurrence of the individual life forms. Some show a decrease as we go upwards, others increase, and others again are constant. The H percentage is fairly constant through all zones, c. 50. Pt, G, HH and Th decrease strongly as we go upward; above the 800 m curve these types have only been noted a few times. With respect to their content of these life forms, various differences may be shown to exist between the various zones, and possibly the highland tracts between 300 and 800 m may by means

TABLE 3.

The Biological Spectra of Iceland.

	N	Pt	n	Ph	Ch	H	G	HH	Th
11—1200 m.....	28	3.7	27	>	44.4	44.4	7.4	>	3.7
10—1100 -	20	>	20	>	50.0	40.0	10.0	>	>
9—1000 -	28	3.7	27	>	40.7	51.9	7.4	>	>
8—900 -	26	>	26	>	42.3	50.0	7.7	>	>
7—800 -	65	3.2	63	>	36.5	46.0	12.7	1.6	3.2
6—700 -	91	2.2	89	>	29.2	53.9	11.2	3.4	2.2
5—600 -	117	4.5	112	>	25.0	56.3	8.9	5.4	4.5
4—500 -	161	5.2	153	0.7	21.6	54.9	12.4	5.2	5.2
3—400 -	204	7.9	189	1.1	20.1	51.9	12.2	5.8	9.0
Tvídígra.....	126	5.0	120	0.8	25.0	50.0	12.5	7.5	4.2
Mývatn	166	7.8	154	0.6	24.0	46.1	13.6	6.5	9.2
East Iceland	272	6.3	256	0.8	18.0	51.2	12.5	7.4	10.2
North Iceland.....	331	7.5	308	1.0	16.6	52.3	11.0	9.1	10.1
Vestfirðir	277	8.2	256	0.8	16.0	53.9	12.5	6.6	10.2
SW Iceland.....	314	8.3	290	0.7	15.2	51.4	11.4	9.3	12.1
South Iceland.....	309	6.2	291	1.0	15.1	52.2	11.3	8.9	11.3
The Highland tracts 8—1200..	40	5.2	38	>	34.2	52.6	10.5	>	2.6
— — — 3—800..	224	7.7	208	1.0	21.2	52.9	11.5	5.3	8.2
The whole of Iceland	375	7.4	349	1.1	15.2	52.4	10.6	9.2	11.5
The Highland tracts 8—1200 .	102	2.0	100	>	44.0	47.0	8.0	>	1.0
— — — 3—800..	638	5.3	606	0.5	24.4	53.1	11.6	4.8	5.6
The whole of Iceland	1503	5.8	1401	0.9	16.1	52.2	11.7	8.2	10.8

of these differences be divided into a lower zone rich in G and HH, and an upper zone in which these types grow rarer. Ph are only sparingly represented in the lowest zones. Ch are of the greatest interest. In the lowest zone, between 300 and 400 m, the Ch percentage is 20.1; in the next, 21.6, and henceforth there is a marked increase 25.0—29.2—36.5, until, in the zones above the 800 m curve, we get a Ch percentage varying between 40 and 50 for the individual zones. For the whole highland tract the Ch percentage is 21.2.

By means of the life forms it is thus possible to divide the highland tracts of Iceland into zones delimited and characterised by the percentage content of the individual life forms. It must, however, be reserved for future and more thorough-going investigations to do this as also to draw a comparison between the Icelandic zones on the one hand, and the Scandinavian and Alpine

zones on the other hand. The above-mentioned facts may, however, be utilised to fix one biological line of demarkation in Iceland, viz. *the 20 p. c. Ch biochore*. The lowest zone, the 300—400 m zone, has a Ch percentage of 20.1. The Ch percentage in the lowlands is below 20, and as it is a rule that species decrease in number as we go upward, while only a few or no species are added from above, the 20 p. c. Ch biochore may with fair accuracy be put at the lower limit of the zone, i. e. at c. 300 m above sea level.

If we compare the position of the 20 p. c. Ch biochore in Iceland with the position of this line in other regions, we shall find very good agreement. In Scotland, according to Raunkiær (1908), the 20 p. c. Ch biochore lies at a height of c. 800 m above sea level, and in the Faeroes at c. 500 m. In Greenland only the southernmost part, 61—60° N., lies south of the 20 p. c. Ch biochore. In other words, here the line has come down to sea level. Hence the position in Iceland of the 20 p. c. Ch biochore at an altitude of c. 300 m is in very good agreement with facts in the surrounding countries.

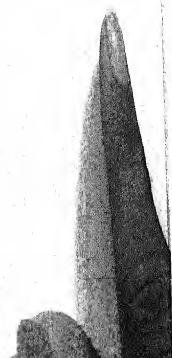
That Ch is the life form best adapted to the Icelandic climate will also appear from the lists in another way. It is clear from the way in which the spectra are calculated that the rarer species will easily come to dominate too much. This error may, however, be rectified by comparing the spectrum formed for a series of zones in the usual way with the spectrum which may be formed from the total of the notes for all zones. Below in table 3 this has been done for Iceland as a whole, for the highland tracts between 300 and 800 m, and for the tracts between 800 and 1200 m. It will appear from the table with all desirable plainness that Ch show the best adaptation, H are indifferent, and Pt, F, HH and Th show the poorest adaptation to the Icelandic climate. The geophytes present interesting facts. In the lowlands they are best adapted to the climate, in the highland tracts between 300 and 800 m they are indifferent, while above the 800 m curve, similarly to H, they thrive badly.

Though we must thus suppose from the above that Raunkiær's life forms would afford a convenient basis even for a more thorough-going investigation of the flora and vegetation of Iceland, a classification of the flora according to other viewpoints will always be of interest. Hence I have also divided the flora into groups according to the distribution of the species in Europe and the adjacent arctic

regions. For we cannot take it for granted that a species, because it has come to a certain region, will at once assume the most pronounced life form of the region in question. The dominating life form in arctic regions is Ch, yet we find species with another life form, and these species must be supposed to be just as well adapted to arctic regions as several of the chamaephytes growing there. Conversely, in regions having a hemicryptophyte climate, we may find Ch. A species like *Calluna vulgaris* must be assumed to be just as well adapted to the Danish climate as many hemicryptophytes. Even though Raunkiær's life forms give an excellent biological picture of the climate, they do not give the most accurate picture of it. The distribution of the species must rank first in this respect. However, there must be no disagreement between results obtained by means of Raunkiær's life forms and those obtained by investigations based on the geographical distribution of the species, though at the outset we must expect the latter to give the more pronounced result. Raunkiær's life forms picture the morphological adaptation of the species, the species groups give expression to their physiological adaptation, both, however, express their adaptation to the same life conditions.

Various enquirers in various countries have at different times worked out a classification of the floras of their respective countries. Thus Watson divided the British flora into groups according to the geographical distribution of the species. A. Blytt divided the Norwegian flora on a somewhat similar principle, and various Swedish enquirers, i. a. Gunnar Andersson and H. Hesselman, have classified the Swedish flora. Ostenfeld has classified the flora of the Faeroes, Porsild and Ostenfeld the Greenlandish flora. The principle acted upon by all these enquirers was to separate all species having a pronounced northern or southern distribution from all such as showed an equal distribution over the entire area. This resulted in the first instance in the setting up of three groups, while Watson and Blytt in addition classified the species according as they had a pronounced Atlantic or continental distribution.

An attempt to bring together the species groups of the various authors and thus arrive at a classification of the Icelandic flora proved impossible, since their species groups overlap to such a de-



gree that no satisfactory result was obtainable. I had then no other alternative but to attempt a classification myself. In working out this, an acquaintance with the groups of other authors has of course been of great use to me.

The best way would no doubt be to determine the course of the Ch biochores in the arctic regions and in Europe and next to determine between which biochores the individual Icelandic species most frequently occur, and then classify the flora on the basis of these data. This work I began but had to give it up again as it took so much time that I dared not at the present juncture embark upon it.

The principles which I then adopted, and on which the classification of the flora given below is based, are the following. First I divided the flora into two larger groups A and E, according as the species were of common occurrence in arctic and subarctic regions but were absent or rare in temperate zones (group A), or the species were common in or typical of the more southerly regions (group E). The A group corresponds approximately to the "arctic species", "alpine species", "mountain plants" etc. of the various authors, while the E group corresponds to the "British species", "European species", "Northern species", "Southern species", "Lowland species" etc. The distinction between these two groups does not cause any difficulties, these do not appear until we attempt to subdivide them. In the following the A group is subdivided into three minor groups according to the northern limits of the species, or their ability to withstand cold, in such a way that group 3 extends farthest north or highest up the mountains while group 1 stops first, and group 2 occupies an intermediate position. On the same principle group E is subdivided into 4 minor groups, group 4 including the species occurring farthest north and group 1 those occurring farthest south. The Icelandic flora is thus divided into 7 groups according to the distribution of the species and more precisely according to their "temperature demands".

The distribution of the species has been investigated in the following countries: — Ellesmereland, North Greenland, Spitsbergen, West and East Greenland, Iceland, the Faeroes, Norway, Sweden, Finland, Novaia Zemlia, Ireland, Scotland, England, Denmark, the Baltic States, and north-eastern Germany. The works on the respective floras will be found in the bibliography. — In fig. 1 temperature curves for a series of stations along the western coasts of Greenland and Scandinavia are shown.

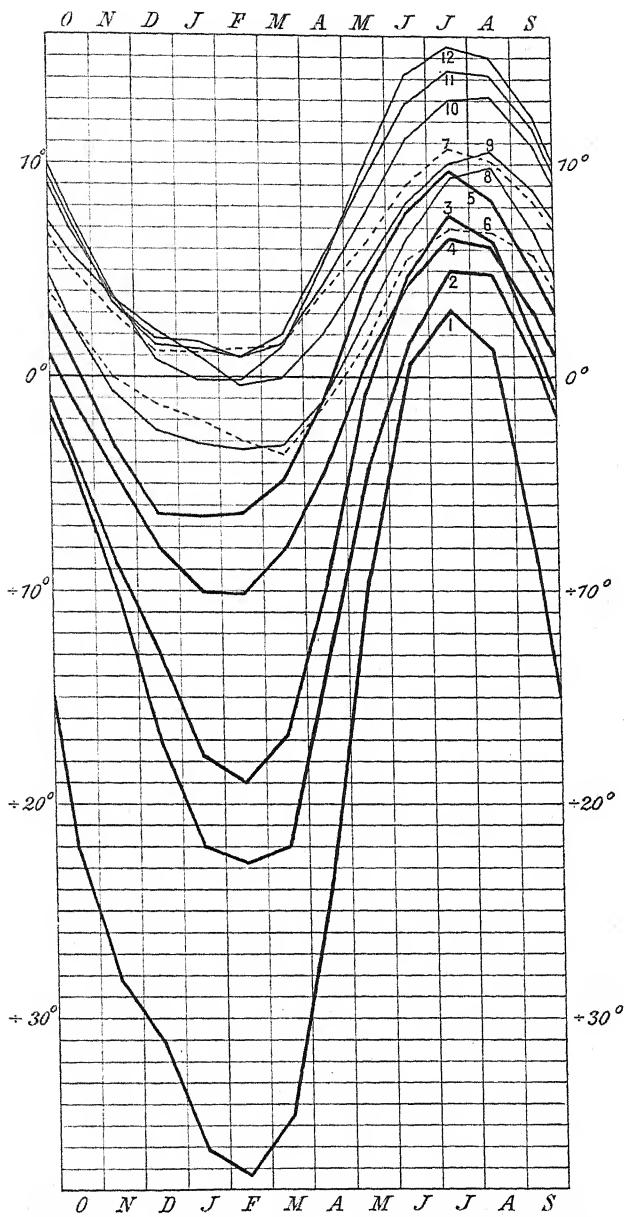


Fig. I. Temperature Curves for a Series of Stations along the Coasts of W. Greenland, Iceland, and Scandinavia. From tables in Hann, 1911.

1. North Greenland: 82° N., 63.7° W. 2. Upernivik $72^{\circ} 47'$ N., $55^{\circ} 53'$ W., 12 m. above sea-level.
3. Jakobshavn $69^{\circ} 13'$ N., $50^{\circ} 55'$ W., 13 m. above sea-level. 4. Godthaab $64^{\circ} 11'$ N., $51^{\circ} 46'$ W., 11 m. above sea-level. 5. Ilivigtut $61^{\circ} 12'$ N., $48^{\circ} 11'$ W., 5 m. above sea-level. 7. Vestmannaeyjar, S. Iceland
6. Grimsey, N. Iceland $66^{\circ} 34'$ N., $18^{\circ} 3'$ W., 2.5 m. above sea-level. 9. Skomvaer $67^{\circ} 24'$ N., $11^{\circ} 54'$ E., 20 m. above sea-level. 10. Christiansund, $63^{\circ} 7'$ N., $7^{\circ} 45'$ E., 15 m. above sea-level. 11. Bergen $60^{\circ} 23'$ N., $5^{\circ} 21'$ E., 20 m. above sea-level. 12. Fansø $55^{\circ} 27'$ N., $8^{\circ} 24'$ E., 5 m. above sea-level.

The 7 species groups contain the following species: —

A 3. Arctic species common in North Greenland north of 76°.

H	<i>Agropyrum violaceum</i>	H	<i>Juncus triglumis</i>
Ch	<i>Antennaria alpina</i>	Th	<i>Koenigia islandica</i>
Ch	<i>Arenaria ciliata</i>	H	<i>Luzula arcuata</i>
Ch	<i>Armeria sibirica</i>	H	<i>Mertensia maritima</i>
H	<i>Campanula uniflora</i>	Ch	<i>Minuartia biflora</i>
H	<i>Cardamine bellidiflora</i>	Ch	— <i>verna</i>
H	<i>Carex capillaris</i>	H	<i>Oxyria digyna</i>
H	— <i>glareosa</i>	H	<i>Papaver radicatum</i>
G	— <i>incurva</i>	H	<i>Pedicularis flammea</i>
H	— <i>nardina</i>	H	<i>Poa glauca</i>
H	— <i>pedata</i>	G	<i>Polygonum viviparum</i>
G	— <i>rigida</i>	H	<i>Ranunculus glacialis</i>
G	— <i>rupestris</i>	HH	— <i>hyperboreus</i>
G	— <i>salina</i>	H	— <i>pygmæus</i>
G	— <i>saxatilis</i>	Ch	<i>Sagina intermedia</i>
H	<i>Catabrosa algida</i>	Ch	<i>Salix glauca</i>
Ch	<i>Cerastium alpinum</i>	Ch	— <i>herbacea</i>
Ch	<i>Draba alpina</i>	H	<i>Saxifraga cernua</i>
Ch	— <i>nivalis</i>	Ch	— <i>groenlandica</i>
Ch	<i>Dryas octopetala</i>	H	— <i>Hirculus</i>
H	<i>Elyna Bellardi</i>	H	— <i>nivalis</i>
H	<i>Epilobium latifolium</i>	Ch	— <i>oppositifolia</i>
	<i>Equisetum variegatum</i>	H	— <i>rivularis</i>
H	<i>Erigeron uniflorus</i>	H	— <i>stellaris</i>
HH	<i>Eriophorum Scheuchzeri</i>	Ch	<i>Silene acaulis</i>
H	<i>Juncus biglumis</i>	Ch	<i>Stellaria humifusa</i>
H	— <i>castaneus</i>	H	<i>Trisetum spicatum</i>

Woodsia ilvensis.

A 2. Arctic Species whose Northern Limit in West Greenland lies between 66° and 76° N.

Ch	<i>Alchemilla alpina</i>	Ch	<i>Cassiope hypnoides</i>
H	— <i>glomerulans</i>	Ch	<i>Cerastium trigynum</i>
H	<i>Arabis alpina</i>	G	<i>Corallorrhiza innata</i>
H	<i>Archangelica officinalis</i>	H	<i>Deschampsia alpina</i>
H	<i>Bartschia alpina</i>	Ch	<i>Diapensia lapponica</i>
Ch	<i>Betula nana</i>	H	<i>Draba incana</i>
Ch	<i>Bryanthus coeruleus</i>	H	<i>Epilobium anagallidifolium</i>
H	<i>Carex alpina</i>	Th	<i>Euphrasia latifolia</i>
H	— <i>bicolor</i>	Th	— <i>nivalis</i>
H	— <i>brunnescens</i>	Th	— <i>serrata</i>
H	— <i>capitata</i>	Th	— <i>tenella</i>
G	— <i>festiva</i>	Ch	<i>Gnaphalium supinum</i>
H	— <i>lagopina</i>	H	<i>Hieracium alpinum</i>
G	— <i>microglochin</i>	G	<i>Juncus arcticus</i>
G	— <i>rariflora</i>	H	— <i>trifidus</i>

Ch	<i>Loiseleuria procumbens</i>	Ch	<i>Saxifraga Aizoon</i>
H	<i>Luzula spicata</i>	H	<i>Sedum villosum</i>
	<i>Lycoptodium alpinum</i>	Ch	<i>Sibbaldia procumbens</i>
Ch	<i>Minuartia stricta</i>	HH	<i>Sparganium submuticum</i>
H	<i>Phleum alpinum</i>	H	<i>Stellaria borealis</i>
Th	<i>Pleurogyne rotata</i>	H	<i>Taraxacum croceum</i>
H	<i>Poa alpina</i>	H	<i>Thalictrum alpinum</i>
H	<i>Potentilla verna</i>	H	<i>Tofieldia borealis</i>
K	<i>Rhodiola rosea</i>	H	<i>Veronica alpina</i>
Ch	<i>Saxifraga aizoides</i>	Ch	— <i>fruticans</i>
			<i>Viscaria alpina.</i>

A 1. Arctic-Subarctic Species whose Northern Limit in West Greenland lies between 60 and 66° N.

H	<i>Alchemilla acutidens</i>	H	<i>Hieracium arctocerinthe</i>
H	— <i>faeroensis</i>	H	— <i>dovrense</i>
Ch	<i>Arabis petraea</i>	H	— <i>islandicum</i>
	<i>Athyrium alpestre</i>	H	— <i>nigrescens</i>
	<i>Botrychium lanceolatum</i>	H	— <i>prenanthoides</i>
H	<i>Carex atrata</i>	H	— <i>strictum</i>
G	— <i>chordorrhiza</i>		<i>Isoetes echinospora</i>
HH	— <i>norvegica</i>	G	<i>Juncus balticus</i>
G	— <i>sparsiflora</i>	G	<i>Listera cordata</i>
Ch	<i>Cerastium nigrescens</i>	H	<i>Luzula sudetica</i>
H	<i>Cornus suecica</i>	H	<i>Poa laxa</i>
Ch	<i>Draba rupestris</i>	H	<i>Primula stricta</i>
	<i>Dryopteris lonchitis</i>	Th	<i>Rhinanthus groenlandica</i>
H	<i>Epilobium alsinifolium</i>	Ch	<i>Sagina Linnæi</i>
H	— <i>Hornemannii</i>	Ch	<i>Salix lanata</i>
H	— <i>lactiflorum</i>	Ch	— <i>phylicifolia</i>
H	<i>Erigeron borealis</i>	Ch	<i>Saxifraga Cotyledon</i>
H	<i>Galium trifidum</i>	Ch	— <i>hypnoides</i>
Th	<i>Gentiana aurea</i>	Th	<i>Sedum annuum</i>
H	<i>Gnaphalium norvegicum</i>		<i>Selaginella selaginoides</i>
G	<i>Habenaria viridis</i>	H	<i>Sesleria coerulea</i>
H	<i>Haloscias scoticum</i>	Ch	<i>Silene maritima</i>
		H	<i>Stellaria crassifolia.</i>

E 4. European Species whose Northern Limit in West Greenland lies north of 66° N.

H	<i>Alchemilla minor</i>	H	<i>Cardamine pratensis</i>
H	<i>Alopecurus aristulatus</i>	H	<i>Carex canescens</i>
HH	<i>Batrachium trichophyllum</i>	G	— <i>dioica</i>
	<i>Botrychium Lunaria</i>	H	<i>Cochlearia officinalis</i>
H	<i>Calamagrostis neglecta</i>	HH	<i>Comarum palustre</i>
HH	<i>Callitricha autumnalis</i>		<i>Cystopteris fragilis</i>
HH	— <i>verna</i>		<i>Dryopteris dilatata</i>
H	<i>Campanula rotundifolia</i>	G	<i>Elymus arenarius</i>

Ch	<i>Empetrum nigrum</i>	G	<i>Poa pratensis</i>
H	<i>Epilobium angustifolium</i>	Th	<i>Polygonum aviculare</i>
	<i>Equisetum arvense</i>	HH	<i>Potamogeton alpinus</i>
G	<i>Eriophorum polystachyum</i>	HH	— <i>tiliformis</i>
H	<i>Festuca ovina</i>	HH	— <i>gramineus</i>
H	— <i>rubra</i>	HH	— <i>pusillus</i>
G	<i>Habenaria albida</i>	H	<i>Potentilla anserina</i>
HH	<i>Hippuris vulgaris</i>	H	<i>Puccinellia retroflexa</i>
H	<i>Honekenya peploides</i>	Th	<i>Radicula islandica</i>
H	<i>Juncus supinus</i>	H	<i>Ranunculus acer</i>
Ch	<i>Juniperus communis</i>	H	— <i>reptans</i>
Th	<i>Limosella aquatica</i>	H	<i>Rumex acetosella</i>
	<i>Lycopodium annotinum</i>	HH	<i>Scirpus aciculatus</i>
	— <i>selago</i>	H	— <i>cæspitosus</i>
HH	<i>Menyanthes trifoliata</i>	Th	<i>Stellaria media</i>
Th	<i>Montia rivularis</i>	Ch	<i>Thymus serpyllum</i>
HH	<i>Myriophyllum spicatum</i>	H	<i>Triglochin palustre</i>
H	<i>Pinguicula vulgaris</i>	HH	<i>Utricularia minor</i>
H	<i>Pirola minor</i>	Ch	<i>Vaccinium uliginosum</i>
Ch	— <i>secunda</i>	Ch	— <i>vitis idaea</i>
H	<i>Plantago maritima</i>		

E 3. European Species whose Northern Limit in West Greenland lies between 60° and 66° N.

H	<i>Achillea millefolium</i>	G	<i>Habenaria hyperborea</i>
H	<i>Agrostis alba</i>	H	<i>Hieracium murorum</i>
H	— <i>canina</i>	H	<i>Juncus alpinus</i>
H	<i>Anthoxanthum odoratum</i>	Th	— <i>bufonius</i>
Th	<i>Atriplex hastata</i>	G	— <i>filiformis</i>
Ph	<i>Betula pubescens</i>	H	<i>Lathyrus maritimus</i>
HH	<i>Callitrichia hamulata</i>	H	<i>Leontodon autumnalis</i>
Th	<i>Capsella bursa pastoris</i>	H	<i>Luzula multiflora</i>
G	<i>Carex Goodenoughii</i>		<i>Lycopodium clavatum</i>
G	— <i>Lyngbyei</i>	H	<i>Matricaria inodora</i>
H	— <i>oederi</i>	HH	<i>Myriophyllum alternifl.</i>
G	— <i>panicea</i>	H	<i>Nardus stricta</i>
HH	— <i>rostrata</i>	Th	<i>Poa annua</i>
H	<i>Catabrosa aquatica</i>	H	— <i>nemoralis</i>
Ch	<i>Cerastium cæspitosum</i>	H	<i>Puccinellia maritima</i>
H	<i>Deschampsia flexuosa</i>	H	<i>Rubus saxatilis</i>
H	<i>Drosera rotundifolia</i>	H	<i>Rumex acetosa</i>
	<i>Dryopteris filix mas</i>	H	— <i>domesticus</i>
	— <i>phegopteris</i>	H	<i>Sagina nodosa</i>
	— <i>pulchella</i>	H	— <i>procumbens</i>
	<i>Equisetum hiemale</i>	G	<i>Scirpus palustris</i>
H	<i>Epilobium palustre</i>	H	— <i>pauciflorus</i>
H	<i>Geranium sylvaticum</i>	HH	<i>Sparganium affine</i>
Th	<i>Gnaphalium uliginosum</i>	Th	<i>Subularia aquatica</i>

Ch	<i>Vaccinium oxycoccus</i>	H	<i>Viola palustris</i>
H	<i>Vicia cracca</i>	HH	<i>Zostera marina</i>
H	<i>Viola canina</i>		

E 2. European Species absent from Greenland but without any Northern Limit in Scandinavia.

H	<i>Agrostis tenuis</i>	H	<i>Milium effusum</i>
H	<i>Alopecurus geniculatus</i>	Th	<i>Myosotis arvensis</i>
H	<i>Angelica silvestris</i>	G	<i>Orchis maculatus</i>
H	<i>Arachnites paludosum</i>	H	<i>Oxalis acetosella</i>
Ch	<i>Arctostaphylos uva ursi</i>	G	<i>Paris quadrifolia</i>
	<i>Athyrium filix femina</i>	H	<i>Parnassia palustris</i>
Th	<i>Cakile maritima</i>	H	<i>Pirola rotundifolia</i>
Ch	<i>Calluna vulgaris</i>	H	<i>Plantago major</i>
H	<i>Caltha palustris</i>	H	<i>Poa trivialis</i>
G	<i>Carex limosa</i>	Ph	<i>Populus tremula</i>
H	<i>Carum carvi</i>	HH	<i>Potamogeton perfoliatus</i>
H	<i>Deschampsia cespitosa</i>	H	<i>Ranunculus repens</i>
	<i>Equisetum limosum</i>	Th	<i>Rhinanthus crista galli</i>
	— <i>palustre</i>	Ph	<i>Sorbus aucuparia</i>
	— <i>pratense</i>	Th	<i>Spergula arvensis</i>
Th	<i>Erysimum hieracifolium</i>	H	<i>Spiraea ulmaria</i>
Th	<i>Galeopsis Tetrahit.</i>	H	<i>Taraxacum vulgare</i>
H	<i>Galium boreale</i>	G	<i>Trientalis europaea</i>
H	— <i>uliginosum</i>	H	<i>Trifolium repens</i>
H	<i>Gentiana amarella</i>	H	<i>Triglochin maritimum</i>
H	<i>Geum rivale</i>	H	<i>Urtica dioica</i>
H	<i>Glaux maritima</i>	Th	— <i>urens</i>
H	<i>Hieracium sylvaticum</i>	Ch	<i>Vaccinium Myrtillus</i>
G	<i>Hierochloë odorata</i>	Ch	<i>Veronica officinalis</i>
H	<i>Lathyrus palustris</i>	H	— <i>scutellata</i>
Th	<i>Melampyrum sylvaticum</i>	H	— <i>serpyllifolia</i>

E 1. European Species with a distinct Northern Limit in Scandinavia.

H	<i>Agropyrum caninum</i>	Th	<i>Crassula aquatica</i>
G	— <i>repens</i>	H	<i>Epilobium collinum</i>
H	<i>Anthyllis vulneraria</i>	Th	<i>Erophila verna</i>
H	<i>Avena elatior</i>	H	<i>Festuca pratensis</i>
	<i>Blechnum spicant</i>	H	<i>Fragaria vesca</i>
H	<i>Brunella vulgaris</i>	H	<i>Galium silvestre</i>
HH	<i>Callitricha stagnalis</i>	H	— <i>verum</i>
Th	<i>Cardamine hirsuta</i>	H	<i>Gentiana campestris</i>
H	— <i>sylvatica</i>	HH	<i>Glyceria fluitans</i>
G	<i>Carex glauca</i>	H	<i>Gnaphalium sylvaticum</i>
H	— <i>paniculata</i>	H	<i>Hieracium Schmidti</i>
H	— <i>pilulifera</i>	H	<i>Hydrocotyle vulgaris</i>
G	<i>Cirsium arvense</i>	H	<i>Juncus lamprocarpus</i>

H	<i>Knautia arvensis</i>	Th	<i>Polygonum persicaria</i>
Th	<i>Lamium intermedium</i>	HH	<i>Potamogeton natans</i>
H	<i>Lathyrus pratensis</i>	Ph	<i>Rosa canina</i>
Th	<i>Linum catharticum</i>	Ch	— <i>spinossissima</i>
G	<i>Listera ovata</i>	HH	<i>Ruppia maritima</i>
H	<i>Litorella uniflora</i>	H	<i>Sagina subulata</i>
H	<i>Lychnis flos eculi</i>	H	<i>Sangivisorba officinalis</i>
Th	<i>Myosotis hispida</i>	Ch	<i>Sedum acre</i>
Th	— <i>micrantha</i>	Th	<i>Senecio vulgaris</i>
Th	— <i>versicolor</i>	Th	<i>Sisymbrium sophia</i>
HH	<i>Myriophyllum verticillatum</i>	HH	<i>Sparganium minimum</i>
	<i>Ophioglossum vulgatum</i>	H	<i>Succisa pratensis</i>
G	<i>Orchis latifolius</i>	H	<i>Valeriana officinalis</i>
H	<i>Phleum pratense</i>	HH	<i>Veronica anagallis</i>
H	<i>Plantago lanceolata</i>	H	<i>Vicia sepium</i>
	<i>Polypodium vulgare</i>	H	<i>Viola silvestris</i>
HH	<i>Polygonum amphibium</i>	Th	— <i>tricolor</i>
		HH	<i>Zannichellia palustris.</i>

On the basis of particulars as to the proportion of each species in the floras of the above-mentioned countries, the Icelandic species were referred to one of the 7 species groups. While it is comparatively easy to place the species in the A or E groups, as this is only a question of ascertaining whether the main distribution of the species is above or below, north or south of three limits, the 20% Ch biore, a subdivision at the outset necessitates the selection of a parallel of latitude, to the north of which the species do not occur. At each species group is stated the parallel of latitude selected as the upper limit of the species. In order to gain a comprehensive view of the extent to which it has been possible to gather the species into groups expressing adaptation to the arctic climate, the following conditions have been reviewed: — 1) The presence of the species groups in the floras of the different countries, 2) the distribution of the groups in Iceland, and 3) the content of Raunkiær's life forms in each group.

I. In table 4 are given the individual countries examined, beginning with those that are most arctic in character, as Ellesmere-land, North Greenland, and Spitsbergen, and ending with the most temperate. In the first column is stated the number of species which the country in question has in common with Iceland. The next two columns state how many of these species, common to both, belong to the A- and E-groups, and the last columns give particulars of the sub-groups.

TABLE 4.

**Distribution of the Species Groups in Northern Europe
and the Arctic Regions.**

	n	A	E	A3	A2	A1	E4	E3	E2	E1
Ellesmereland	55	45	10	43	2	»	10	»	»	»
North Greenland 76°—83°—76°	66	51	15	51	»	»	15	»	»	»
Spitsbergen	53	43	10	43	»	»	10	»	»	»
West Greenland 66°—76° . . .	170	111	59	55	50	6	57	2	»	»
East Greenland 60°—76° . . .	177	117	60	53	46	18	44	15	»	1
Novaia Zemlia	72	51	21	36	12	3	17	2	2	»
South-West Greenland 60°—66°	228	121	107	50	49	22	53	53	1	»
Iceland	375	151	224	55	51	45	57	53	53	61
The Faeroes	219	73	146	27	21	25	45	38	29	34
Norway	367	144	223	54	50	40	57	52	53	61
Sweden	363	141	222	52	49	40	57	51	53	61
Finland	344	132	212	52	45	35	57	50	53	52
Scotland	304	86	218	28	32	26	56	50	52	60
Iceland	243	36	207	14	8	14	52	49	48	58
England	231	20	211	8	5	7	53	49	51	58
Denmark	238	17	221	5	2	10	57	51	53	60
The Baltic States	231	20	211	6	5	9	53	50	53	55
North-East Germany	231	15	216	3	3	9	55	50	53	58

In the countries north of Iceland it is especially the A species which constitute the greater part of the common species, and the farther north we go, the more numerous are the A 3 species.

In the countries south of Iceland the reverse is the case; here comparatively the greatest number of the common species belongs to the E groups. In Scandinavia and Finland the proportion of the A groups to the E groups is approximately as in Iceland.

The table shows the distribution of the species groups illustrated exclusively by the quantitative relation of the species to each other. The facts relating to the distribution would, however, appear much more distinctly if the frequency of the species in the separate countries were taken into account, and a classification were worked out for Scandinavia.

II. The Distribution of the Species Groups in Iceland.

Below in table 5 the quantitative relation between the species groups has been calculated in per cent partly of the number of

TABEL 5. Distribution of the Species Groups in Iceland.

	n	A	E	A3	A2	A1	E4	E3	E2	E1
11—1200 m.....	28	78.6	21.4	57.1	10.7	10.7	17.9	3.6	2	2
10—1100 -	20	85.0	15.0	65.0	10.0	10.0	15.0	2	2	2
9—1000 -	28	82.1	17.9	57.1	14.3	10.7	14.3	3.6	2	2
8—900 -	26	88.5	11.5	65.4	11.5	11.5	11.5	2	2	2
7—800 -	65	80.0	20.0	44.6	24.6	10.8	18.5	1.5	2	2
6—700 -	91	73.6	26.4	35.2	25.3	13.2	20.9	4.4	1.1	2
5—600 -	117	69.2	30.8	29.1	28.2	12.0	19.7	6.8	3.4	0.9
4—500 -	161	59.6	40.4	23.6	24.8	11.2	18.6	13.0	7.5	1.2
3—400 -	204	49.5	50.5	19.6	20.1	9.8	18.6	15.2	13.7	2.9
Tvidægra	126	57.9	42.1	21.4	25.4	11.1	21.4	14.3	5.6	0.8
Mývatn	166	50.6	49.4	18.7	20.4	11.4	19.3	16.3	11.4	2.4
East Iceland	272	45.2	54.8	16.5	17.3	11.4	16.9	17.3	13.2	7.4
North Iceland	331	44.4	55.6	16.3	15.1	13.0	17.2	15.1	13.0	10.3
Vestfirðir	277	43.7	56.3	15.5	15.9	12.3	18.1	16.6	14.4	7.2
South-West Iceland	314	40.4	59.6	13.7	14.3	12.4	16.9	16.2	14.0	12.4
South Iceland	309	39.2	60.8	13.9	13.9	11.3	17.2	15.5	13.9	14.2
The highland tracts 8—1200 m	40	80.0	20.0	57.5	12.5	10.0	15.0	5.0	2	2
— — — 3—800 -	224	51.8	48.2	20.1	20.5	11.2	17.4	15.2	12.9	2.7
The whole of Iceland	375	40.3	59.7	14.6	13.6	12.0	15.2	14.1	14.1	16.3
The highland tracts 8—1200 m	102	83.3	16.7	60.8	11.8	10.8	14.7	2.0	2	2
— — — 3—800 -	638	62.2	37.8	27.1	24.0	11.1	19.1	10.2	7.1	1.4
The whole of Iceland	1503	42.5	57.5	15.2	15.2	12.1	17.2	16.1	13.7	10.4

species, partly of the number of points 1) for the whole of Iceland, which means, practically, for the lowlands of Iceland, 2) for the highland tracts between the 300 and 800 m curves, and, finally, 3) for the highland tracts between the 800 and 1200 m curves. It appears from the table with all desirable plainness that the A group is best adapted to Icelandic conditions, considerably better than the E group. This is evident both from the values computed from the species figures and those computed from the points, but it is especially evident on comparison between the percentages within the same altitude group.

If, next, we consider the subgroups, the table shows a gradual adaptation to arctic conditions. E 2 and especially E 1 show the poorest adaptation, not even the lowlands seem to offer favourable conditions for the species of these two groups. E 3 thrives well here,

TABLE 6.

Quantitative Distribution of the Species Groups in Iceland.

		The entire flora	A	E	A3	A2	A1	E4	E3	E2	E1
number of species	375	151	224	55	51	45	57	53	53	61
East Iceland.....	absent	27.5	18.6	33.5	18.2	7.8	31.1	19.3	11.3	32.1	67.2
	scattered-rare	27.5	25.8	28.5	27.3	23.5	26.7	15.8	35.9	37.8	26.3
	common	45.1	55.6	38.0	54.5	68.6	42.2	64.9	52.8	30.2	6.6
North Iceland	absent	11.7	2.6	17.9	1.8	2.0	4.4	>	5.7	18.9	44.3
	scattered-rare	40.8	37.1	43.3	40.0	25.4	46.6	36.8	37.7	49.1	49.7
	common	47.5	60.3	38.8	58.2	72.6	48.9	63.1	56.6	32.1	6.6
North-West Iceland .	absent	26.1	19.9	30.4	21.8	13.7	24.4	12.3	13.2	24.5	67.2
	scattered-rare	32.0	28.5	34.4	23.7	25.5	37.7	26.3	35.8	49.1	27.9
	common	41.9	51.7	35.3	54.5	60.8	37.8	61.4	51.0	26.4	5.0
South-West Iceland .	absent	16.3	15.9	16.5	21.8	11.8	13.3	7.0	3.8	17.0	36.1
	scattered-rare	37.3	30.5	42.0	23.7	23.6	46.7	28.1	37.7	45.3	55.7
	common	46.4	53.6	41.5	54.5	64.7	40.0	64.9	58.5	37.7	8.2
South Iceland	absent	17.6	19.9	16.1	21.8	15.7	22.2	7.0	9.4	18.9	27.9
	scattered-rare	37.3	27.8	43.8	23.7	23.6	37.8	33.3	39.6	45.3	55.7
	common	45.1	52.3	40.2	54.5	60.8	40.0	59.6	51.0	35.9	16.4
Average	absent	19.8	15.4	22.9	17.1	10.2	19.1	9.1	8.7	22.3	48.5
	scattered-rare	35.0	30.0	38.4	27.7	24.3	39.1	28.1	37.3	45.3	42.9
	common	45.2	54.7	38.8	55.2	65.5	41.8	62.8	54.0	32.5	8.6

but conditions even in the lower areas of the highland tracts are unfavourable to this group. For E 4 this is not the case until we reach the upper areas of the highlands. In the lower highland tracts this group even seems to thrive better than in the lowlands. The same is the case with the subgroups of A. A 1 is mainly indifferent though it occurs most frequently in the lowlands, A 2 exhibits the highest percentage in the lower highland tracts, but in any case finds the upper highland tracts unfavourable, while A 3 shows the absolutely highest percentage in that area.

Between A 3 as one extreme and E 1 as the other the remaining groups show a fairly smooth gradation.

In Stefán Stefánsson's »Flóra Íslands« it is stated for each species with what degree of commonness it occurs in each of the 5 parts

of the country E., N., N. W., S. W., and S. Iceland. The designation algeng, hjer & hvar, or sjaldgæf after each species denotes whether the species is common, scattered or rare. For each of the 5 parts of the country have been added up the species of the respective groups 1) which are absent, 2) which are scattered to rare or 3) which are common within the area. The investigation has been carried out for the flora as a whole, for the main groups, A and E, and for the sub-groups under these two groups, and the result expressed in percent of the species number of the group in question has been given in table 6. The means for all parts of the country are given below in the table. The A group has more common species, less rare or absent species than the E group; while on an average 15,4 p. c. of the species of the A group are absent in each part of the country, the same figure for the E group is 22,9 p. c. For the commonly occurring species the proportion of A to E is as 54.7 to 38.8.

If next we turn to the subgroups, the table shows that A 2 has the greatest number of common species, while A 3 and especially A 1 show a smaller number. Of the E subgroups, E 4 has the greatest number of common species, 62,8 p. c., E 1 the smallest number, 8,6 p. c. E 3 and E 2 occupy an intermediate position with 54,0 p. c. and 32,5 p. c. respectively of common species. The numerical values for the rarer and absent species entirely confirm the sequence. In addition the table shows the quantitative conditions of the flora and species groups in the 5 Icelandic areas. The A group occurs most frequently to the east and north, the E group to the south and south-west. In the A group this is due especially to A 2, in the E group, to E 2 and E 1.

Aided by the above-mentioned tables we can now give the following description of the distribution of the Icelandic species groups in northern Europe and the arctic regions.

The **E group** comprises species of common occurrence in Central Europe. The species have their main distribution to the south of or below the forest limit, the 20 p. c. Ch biochore. The various species, however, transcend this limit in varying degree in consequence of which the following 4 subgroups may be distinguished.

E 1 requires the greatest amount of heat. In England, Denmark, northern Germany, and southern Scandinavia the E 1 species are of common occurrence. In Finland they only occur in the most southerly part, in northern Scandinavia only or principally on shel-

tered sunny slopes. In Iceland most of the E 1 species are rare, they only occur in the lowlands especially towards the south, and thrive best near the hot springs.

E 2. Like the E 1 species, the species of this group are restricted to the lowlands in Iceland, and occur more commonly south of than north of the »jökull line«. However, these species occur more commonly than the species of the previous group. In Scandinavia and Finland they extend right up to the northern coasts, but none of them have reached Greenland.

E 3. Like E 2 the species of this group have no northern limit in Scandinavia and Finland. In Iceland they are common lowland species which still thrive well in the lower zone of the highlands but disappear higher up; they occur commonly and with equal frequency in the various parts of the country. The species are found in South Greenland as pronounced southern types. 66° N. has been chosen as the northern limit of the group in West Greenland.

E 4 is the subgroup which has most common species in Iceland, and the species are of common occurrence right up into the upper zone of the highland tracts. In Greenland, too, the species are of common occurrence, some species even extend right up into North Greenland.

The A group comprises arctic and subarctic species having their main distribution near, north of, or above the forest limit, the 20 % Ch biochore. The species are common in Greenland, Spitsbergen, Iceland, and on the Scandinavian and Scotch mountains. In more southerly countries the species are either absent (and this applies to the majority), or they occur sporadically and in small quantity.

A 3 comprises the species which extend farthest north in the arctic region and are therefore capable of withstanding the severest cold. In Scandinavia these species are confined to the most markedly arctic localities; in Iceland they are a characteristic feature of the upper highland zone.

A 2 comprises most of the common species of the A groups in Iceland. The species of this group are more in evidence north of than south of the "jökull line" and seem to thrive better in the lower highland tracts than above and below. In Greenland these species are of common occurrence though they do not, like the A 3 species, extend into North Greenland.

A 1 comprises such species as must be termed arctic though they do not extend very far north in Greenland. Their northern limit in West Greenland lies south of 66° N. In Iceland the species are equally distributed through all altitude zones, though with a slight maximum in the lowlands. The A 1 species occur most commonly north of the "jökull line", especially in North Iceland.

III. Investigation of the distribution of the species, partly in the North European and the adjacent arctic countries, and partly in Iceland, gave the result that the 7 subgroups show a fairly smooth gradation from A 3, which is adapted to the coldest conditions, to E 1, which requires the greatest amount of heat. The increasing adaption to arctic conditions may, however, be demonstrated in another way, too, viz. by a comparison of the individual groups with respect to their content of Raunkiær's life forms. If the groups and subgroups express an increasing degree of adaption to the arctic climate, this must appear by the fact that that group or those groups which are best adapted to the arctic climate shows or show the greatest content of arctic life forms and fewest temperate life forms, whereas the reverse must be the case with the remaining groups.

Against each species in the above list is given the life form of the species in question, and in table 7 are stated the biological spectra of the groups.

According to Raunkiær (1908, 1912), Ch is the life form which is best adapted to the arctic climate, while H and G are indifferent, and Ph, HH, and Th are adapted to non-arctic conditions. By comparison of the biological spectra of the A and E groups with the spectrum of the entire flora, it will be seen that the A group is more arctic in character, the E group more temperate in character than the flora as a whole. The subgroups under A and E bear the same relation to their respective main groups as these to the whole flora. The high HH percentage in E 4 and partly also in E 1 is however, worth noting.

On reviewing the biological spectra of the various parts and zones of Iceland we saw that the Ch % was lowest (15 %) in the south country where the amount of warm water at the coasts was greatest, that it then rose gradually as the amount of Polar water

TABLE 7. The Biological Spectra of the Species Groups.

	Pt	n	Ph	Ch	H	G	HH	Th
The whole flora.....	7.4	349	1.1	15.2	52.4	10.6	9.2	11.5
A-Group.....	5.6	143	2	26.6	53.1	11.2	2.8	6.3
E-Group.....	8.7	206	1.9	7.3	51.9	10.2	13.6	15.0
A 3.....	3.8	53	2	30.2	52.8	11.3	3.8	1.9
A 2.....	4.0	50	2	26.0	52.0	10.0	2.0	10.0
A 1.....	12.5	40	2	22.5	55.0	12.5	2.5	7.5
E 4.....	11.8	51	2	11.8	43.1	9.8	25.5	9.8
E 3.....	10.4	48	2.1	6.3	56.3	12.5	10.4	12.5
E 2.....	8.2	49	4.1	8.2	59.2	10.2	2.0	16.3
E 1.....	5.2	58	1.7	3.4	50.0	8.6	15.5	20.7

at the coasts increased, and the amount of Gulf Stream water decreased, towards the west and north, until it reached its highest value, 18 p. c. in East Iceland, at the same time as the Polar water became prevalent at the coast. This was the result round the entire coast, and on passing from the level of the sea towards the snow-line the Ch. percentage rose very greatly, from c. 20 p. c. at the 300 m curve to c. 50 p. c. at the snow-line, the 1200 m curve.

If we examine the relations of the species groups under the same conditions, as done in table 5, we find a very close correspondence between the A percentage and the Ch percentage. If we proceed in the same way round the coast from South Iceland via W. and N. to East Iceland, the A percentage shows an unbroken rise from 39.2 p. c. in South Iceland, to 45.2 p. c. in East Iceland, and if we pass from the sea to the snow-line, the same fact appears. The A percentage for the whole country is 40.3, at the 300 m curve it is 49.5, rising to 80 at the snow-line. The table likewise shows the relations of the subgroups. The 20 p. c. Ch biochore seems to coincide with the 50 p. c. A biochore.

Raunkiær's life forms and the phytogeographical species groups thus react similarly to the same external conditions. The species groups are, however, more sensitive than the life forms.

III. TYPES OF ICELANDIC VEGETATION.

THE types of the Icelandic vegetation, their floristic composition, and their distribution in the various parts of Iceland have been treated in a series of works by Chr. Grønlund (1887 and 1884), St. Stefánsson (1895), Helgi Jónsson (1895, 1900, 1905 and 1913), C. H. Ostenfeld (1899 and 1905), Th. Thoroddsen (1914), and Ingimar Óskarsson (1927).

In "The Botany of Iceland" 1914, pp. 317—343, Thoroddsen gives a general view of the types of Icelandic vegetation, attaching to each type a brief discussion of its floristic peculiarities.

According to this the types of vegetation occurring in Iceland are the following:

1. The Vegetation of the Coast Line. a. Rock vegetation, b. fowling cliff vegetation, c. sand strand vegetation, d. salt-marsh vegetation.
2. The Vegetation of Fresh Water. a. Vegetation of running water, b. of lakes and pools.
3. The Vegetation around Springs (the Dý Vegetation).
4. The Vegetation around Hot Springs. a. Around hot alkaline springs, b. around the solfataras.
5. The Vegetation on Wet Soil. a. Mýri vegetation, b. flói vegetation.
6. The Vegetation on Rocky Flats. a. On gravelly flats (melar), b. stone-covered ridges (holt), c. river gravel (urd), d. rocky boulders (hamrar), e. (eyrar), f. clayey flats (flag).
7. The Vegetation of the Mountain Slopes. Under this head come the herb slope and the herb flats.
8. Psammophilous Vegetations. a. Sand-covered tracts (sandar), b. blown sand (dunes).
9. The Vegetation of the Lava Streams; in various stages of development.

10. The *Grimmia* Heath Vegetation.
11. Grassland. a. Grass slopes, b. knolly grassland (*græsmo*), c. dry uncultivated grassland without knolls (*vallendi*), d. the homefield (*útn*).
12. Heather Moors.
13. Willow Copses.
14. Birch Copses and Birch Forests.

The principles on which the above classification has been based take account partly of environment and partly of purely physiognomic features. If, however, a biological point of view is adopted, it will be natural to continue according to the principles employed above in the division of the Icelandic zones of altitude.

In Ingimar Óskarsson's paper on the vegetation and flora in Vestfirðir all the species noted are given under each type of vegetation, and for each species its upper and lower limit. Table 8 below has been worked up from these data and gives both the spectra of the species groups and the biological spectra of the individual altitudinal zones for the whole area and, finally, for the individual types of vegetation.

With regard to the altitudinal zones the table shows a steady decrease in the number of species from below upwards. The biological spectra show a H percentage which is practically constant throughout all zones, but a steadily increasing Ch percentage and steadily decreasing Th, HH, and G percentages from the lower towards the upper zones. The corresponding change in the spectra of the species groups is an increasing excess of A, especially A 3, species, and a steady decrease of E species, the E 1 species disappearing first, the E 4 species last. All these facts are thus in close agreement with those stated for the whole country. — Only the position of the 20 p. c. Ch biochore forms an exception since it lies considerably lower here.

The vegetation spectra have apparently a very variegated appearance. It is, however, possible to combine them to form several characteristic groups. Thus one group comprises the series melar — mo — herb flat, in which the melar vegetation has the highest A percentage and the lowest E percentage. The reverse is the case with the herb flats, while the mo occupies an intermediate position.

Another group consists of the melar — mo — myri and freshwater vegetations. Here the difference is that the melar has the

TABLE 8.

**Species Group Spectra and Biological Spectra of the Altitudinal
Zones and Types of Vegetation in Vestfirðir**
(based on Ingimar Óskarsson's lists of species (1927)).

	n	A	E	A3	A2	A1	E4	E3	E2	E1	Ph	Ch	H	G	HH	Th
4—500 m	14	93	7	50	43	»	7	»	»	»	43	50	7	»	»	»
3—400 -	35	89	11	52	34	3	9	3	»	»	»	43	46	9	3	»
2—300 -	74	68	32	27	27	14	16	14	3	»	»	31	51	14	4	»
1—200 -	112	51	49	21	19	12	22	17	8	2	1	24	46	15	8	5
0—100 -	191	41	59	15	14	12	21	19	14	5	1	17	52	15	6	9
The entire area..	212	44	56	16	16	11	19	18	13	5	1	18	52	14	7	8
Highland melar..	45	82	18	42	31	9	13	4	»	»	»	40	49	11	»	»
Dwarf willow veg.	27	70	30	22	41	7	19	4	7	»	»	30	52	19	»	»
Lowland melar..	82	60	40	22	23	15	17	12	5	6	1	34	54	9	»	2
Heath vegetation.	80	49	51	11	23	15	20	18	11	3	3	25	54	18	»	1
Mo vegetation ...	73	51	49	15	25	11	18	19	8	4	»	22	56	14	»	8
Mýri vegetation..	69	49	51	19	19	12	25	15	10	2	»	10	52	25	9	4
Littoral meadow.	20	50	50	35	5	10	25	25	»	»	»	10	60	15	»	15
Grass-field veg...	57	30	70	7	11	12	18	25	19	9	»	12	60	12	»	16
Herb-field.....	31	32	68	10	23	»	23	26	16	3	»	19	61	16	»	3
Birch copse	47	23	77	4	11	9	26	28	21	2	4	21	40	30	»	4
Freshwater veg...	13	8	92	»	8	»	54	31	8	»	»	»	15	15	70	»
Hot springs	12	»	100	»	»	»	25	42	8	25	»	»	67	8	»	25

highest Ch percentage, the mo the highest H percentage, the mýri the highest G percentage, and the freshwater vegetation the highest HH percentage.

A third group is formed by the littoral vegetation, the grassfield vegetation, and the vegetation of the hot springs. These three types of vegetation are all characterised by a high H percentage and, in proportion to the other types of vegetation and to the area as a whole, an unusually high Th percentage. In the species group spectra, however, they differ essentially.

Between the freshwater vegetation and the vegetation of the hot springs which both show an unusually high E percentage, there is a striking difference in the spectra of the E subgroups, the freshwater vegetation having its maximum in E 4 and the vegetation of the hot springs in E 3. The deviation is, however, greatest in E 1

where the freshwater vegetation is not represented at all, while the hot springs have another maximum here.

In a subsequent chapter I shall return to the vegetation spectra given in table 8. In this connection it will suffice to point out that it is probably the same forces, viz. differences of temperature, which have been active in the formation of the Icelandic types of vegetation which have determined the floristic differences of the altitudinal zones.

The factors especially causing differences of temperature in a given area of Iceland are partly differences with respect to the amount of snow and partly differences with respect to the amount of water. Hence the first task of an analyst of plant formations, after an examination of the vegetation at various heights above sea level, will be to investigate the influence on distribution of these two factors, and by this means attempt a grouping of the Icelandic types of vegetation.

In the two succeeding chapters I shall therefore give a more detailed account of the results I arrived at on analysing the formations on a journey in Iceland in the summer of 1925. In yet another chapter the influence on the vegetation of differences in snow-covering and the moisture of the soil will be more thoroughly discussed, and finally the results thus gained will be utilised in setting up the types of Icelandic vegetation which have, up to the present, been more thoroughly investigated.

An analytical study of the formations has hitherto been carried out in 4 different places in Iceland, viz. on Lýngdalsheiði in Árnessýsla in the south country, partly at c. 100 m above sea level, and further at c. 250—300 m and c. 400 m above sea level; on Arnarvatnsheiði near Úlfsvatn in the highlands northwest of Langjökull at c. 500 m above sea level; in the valley bottom at Lækjamót in Viðidalur in the north country, and in the valley bottom at Norðtunga in Borgarfjörður in the south-west country.

The investigation was carried out by means of Raunkiær's circling method. With a few exceptions, 25 random samples from each locality, each of $\frac{1}{10}$ sq. m., were analysed. I have not thought it appropriate to take into account other methods of analysis, partly because those which could here be considered are of a later date than Raunkiær's circling method and to a certain extent resemble it, partly because, from a scientific point of view, they must be regarded as retrograde. Up to the present, Raunkiær's circling

method is the only method for investigation of the vegetation which, in determining the quantitative distribution of the individual species, makes use of the flora list principle, a principle which has always formed the basis of scientific plant geography, and which must also be adopted in the doctrine of formations if this branch of botany is to lay claim to scientific equality with the other phytogeographical branches of the science.

In naming the individual types of vegetation, I have used the Icelandic names and thus adhered to a custom often adopted in plant geography, that of retaining old names where such were found. At the same time reference of my own more thoroughly investigated types to the previous, more diffusely treated types of vegetation has been avoided, and this is in so far fortunate as it would seem that the latter have been determined with more regard to their physiognomy than to their environment. On the whole, however, the boundary lines coincide. Some of the names have already been used by Helgi Jónsson (1895); for those which do not occur in his paper I am indebted to the courtesy of Icelandic farmers or to Magister Pálmi Hannesson.

IV. THE ICELANDIC LOWLAND FORMATIONS.

A. LÝNGDALSHEIDI.

If from some elevated point, say Hrólfshólar or Thrasaborgir, (cfr. figs. 2 & 3) we try to get a general idea of the vegetation on Lýngdalsheiði, it will, at that distance, appear to us as an immense monotonous greyish green carpet sprinkled with smaller or larger patches of a yellowish or vivid green colour. These three shades of colour answer to the three most widespread types of vegetation on Lýngdalsheiði, viz. the mo, which forms the bulk of the vegetation, the Grimmia heath, mosathembur, which covers the more prominent parts of the landscape as a yellowish carpet, and the snow patches, geiri, which form fresh green oases in the shelter of slopes and hills or in the old beds of rivulets.

This is how the landscape appears in the vegetation period. Earlier in the year, e. g. at the close of the period when the snow melts, the mo and mosathembur vegetations have their natural colour, while the snow still covers the geiri vegetation. In winter the mo as well as the geiri vegetation are covered with snow, while the mosathembur vegetation is bare.

Of less importance than these three types are a few other vegetation types. Where there is a strong wind on the steeper parts, the vegetation and the layer of mould blow away and leave a soil covered with stones and gravel which forms the starting point for the mellar vegetation. On the numerous small cones deposited by the little streams of melting snow, especially in Lyngdal, but also on the flat parts of the volcanic shield we find the vallendi vegetation, and on areas not sufficiently drained there occurs the myri vegetation.

In the following we shall subject these 6 types of vegetation to a closer analysis.

The Mosathembur Vegetation. Cf. fig. 4, and table 9 A-B.

On the more prominent parts of Lýngdalsheiði, from which the snow is at once swept away by the wind in the winter, we find the mosathembur vegetation developed. Even a long distance off this type of vegetation is easily recognisable by its yellowish hue. This colour is due to *Grimmia hypnoides* which covers the surface in a dense and deep elastic carpet. When the Grimmia heath is sufficiently large, the moss carpet is, as it were, split up into large tablets separated by systems of lines; the lines of one system as a rule converge towards a point in the lower edge of the moss carpet, another system forming larger or smaller angles with the first one. These lines do not extend into the surrounding mo, there we find the usual knoll formation.

Table 9 A gives the circling results of the phanerogamous flora of the mosathembur vegetation. The five first columns represent

TABLE 9 A.

The Mosathembur Vegetation on Lýngdalsheiði.

1—5 Localities in Lýngdalur, c. 200 m above sea level, $\frac{2}{7}$ 1925. 6—10. Hrólfsbólar 280—320 m above sea level, $\frac{1}{7}$ 1925. 11 Thrasaborgir, c. 400 m above sea level, $\frac{23}{7}$ 1925. (25. $\frac{1}{10}$ m²)

			1	2	3	4	5	6	7	8	9	10	11
Carex rigida.....	A 3	G	96	88	84	96	96	48	36	56	44	24	32
Salix herbacea.....	A 3	Ch	>	24	4	4	40	100	92	100	100	100	80
Festuca rubra	E 4	H	56	28	44	56	56	>	>	28	>	>	>
Thalictrum alpinum ..	A 2	H	72	20	36	28	48	>	>	24	4	28	
Polygonum viviparum..	A 3	G	8	20	12	>	28	32	28	32	36	48	8
Equisetum pratense....	E 2	G	4	16	>	20	8	>	>	28	8	4	>
Armeria vulgaris	A 3	Ch	>	4	4	8	4	4	8	20	16	12	>
Silene acaulis	A 3	Ch	>	4	>	>	12	4	4	8	16	20	>
Empetrum nigrum.....	E 4	Ch	>	>	>	>	8	8	8	8	12	8	>
Juncus trifidus	A 2	H	>	>	>	>	4	4	8	>	8	4	>
Galium Normanni	A 1	H	8	4	>	>	12	>	>	>	>	>	>
Cerastium alpinum	A 3	Ch	8	4	>	>	12	4	>	>	4	>	>
Festuca ovina	E 4	H	>	>	4	>	>	4	>	>	4	4	>
Loiseleuria procumbens	A 2	Ch	>	>	>	>	>	>	>	>	4	>	>
Luzula spicata.....	A 2	H	>	>	>	>	12	>	>	>	8	4	>
Vaccinium uliginosum .	E 4	Ch	>	>	>	>	>	>	>	>	4	>	>
Equisetum variegatum .	A 3	H	16	>	>	>	>	>	>	>	>	>	>
Rumex acetosa	E 3	H	>	>	4	>	>	>	>	>	>	>	>
Agrostis canina.....	E 3	H	>	>	>	>	4	>	>	>	>	>	>

TABLE 9 B.

Biological Spectra of the Mosathembur Vegetation.

1—11 correspond to 1—11 in table 9 A.

	1	2	3	4	5	6	7	8	9	10	11
Points sum	268	212	192	212	344	208	184	304	268	256	120
Number of species	8	10	8	6	14	9	7	9	14	11	3
Density of species	2.7	2.1	1.9	2.1	3.4	2.1	1.8	3.0	2.7	2.6	1.2
A	77.6	79.2	72.9	64.2	77.9	94.2	95.7	78.9	89.6	93.8	100.0
E	22.4	20.8	27.1	35.8	22.1	5.8	4.3	21.1	10.4	6.3	0.0
A 3	47.8	67.9	54.2	50.9	55.8	92.3	91.3	71.1	80.6	79.7	100.0
A 2	26.9	9.4	18.8	13.2	18.6	1.9	4.3	7.9	9.0	14.1	>
A 1	3.0	1.9	>	>	3.5	>	>	>	>	>	>
E 4	20.9	13.2	25.0	26.4	18.6	5.8	4.3	11.8	7.5	4.7	>
E 3	>	>	>	>	1.2	>	>	>	>	>	>
E 2	1.5	7.5	2.1	9.4	2.4	>	>	9.2	3.0	1.6	>
E 1	>	>	>	>	>	>	>	>	>	>	>
Ch	3.0	17.0	4.2	5.7	22.1	57.7	60.9	44.7	58.2	54.7	66.7
H	56.7	24.5	45.8	39.6	39.5	3.8	4.3	17.1	9.0	15.6	>
G	40.3	58.5	50.0	54.7	38.4	38.5	34.8	38.2	32.8	29.7	33.3
HH	>	>	>	>	>	>	>	>	>	>	>
Th	>	>	>	>	>	>	>	>	>	>	>

mosathembur in Lýngdalur c. 200 m above sea level, 6—10 that of Hrólfsþólar c. 300 m above sea level, and No. 11 that of Thrasaborgir at a level of 400 m.

The phanerogamous vegetation is poor in species and open. In 2.5 sq. m on an average c. 10 species will occur with a density of 2—3.

Biologically the mosathembur vegetation is remarkable by its high percentage of arctic, particularly high arctic, species, and more especially by its high G percentage.

In Lýngdalur, cf. Nos. 1—5, it is H and G that predominate, while Ch is of minor importance. Here the dominant species are *Carex rigida*, *Polygonum viviparum*, *Thalictrum alpinum* and *Festuca rubra*. Higher up, at Hrólfsþólar, H gives place to Ch. Here *Salix herbacea* is the most frequently occurring species. Everywhere throughout the moss carpet this plant sends up the tip of a branch bearing two or three leaves, while the rest of the plant is buried

in the moss. Other species met with are especially *Carex rigida*, *Polygonum viviparum*, *Silene acaulis*, *Armeria* and *Empetrum*. Proceeding still higher, *Salix herbacea* is the only more conspicuous phanerogam in the moss carpet.

At its lower limit the mosathembur vegetation passes over into the Elyna mo.

Above we have described the appearance and composition of the mosathembur vegetation on Lýngdalsheiði. If we enquire into its occurrence in other parts of Iceland, we find it described by Helgi Jónsson for East Iceland (1895, p. 70), for South Iceland (1905, pp. 40—42), and for Snæfellsnes (1900, p. 68 and p. 85). It is most abundantly developed in East Iceland where it covers large stretches of the mountain slopes in several of the fiords, and it is particularly well developed at high levels. In South and South-West Iceland it does not occur so plentifully, and apart from the lava fields, covers only small areas. Its appearance and composition, however, are in close agreement in the various localities and correspond to what was given above for Lýngdalsheiði.

In North Iceland and the highland tracts the mosathembur does not seem to occur as a stable typical vegetation. Ostenfeld does not refer to it in "Skildringer af Vegetationen i Island" III—IV (1905) either from Vestfirðir or from Melrakkasjætta. Personally I have looked for it in vain in Húna Flói, in the highlands at Arnarvatnsheiði, and on Holtavörðuheiði. Typical mosathembur was not seen in any of these localities; it had been replaced by the melar vegetation.

The moss mo observed by St. Stefánsson on Grimstungnaheiði which "should most probably be understood as a transitional form between heather mo and pond vegetation", the surface being uneven, more or less tufted, and the soil moist, at any rate in the first part of the summer, must not be confused with the mosathembur vegetation which only occurs on the relatively dry stretches. Thus, the mosathembur vegetation in Iceland seems to be peculiar to the higher levels of the rainy and foggy east, south, and south-west country, that is to say, the country south of the jökull line. North of this line, where the climate is more continental, it does not occur as the typical vegetation, being replaced by the melar vegetation here.

If we enquire into its distribution in the surrounding countries, we find it developed both to the north and to the south. Kolderup

Rosenvinge records a moss heath from South Greenland (1896, pp. 211—214) which, on p. 214, he refers to the Icelandic *Grimmia* heath. On the distribution of the moss heath the author writes on p. 213, "All the aforementioned localities are situated in the coastal area or not very far from the coast, whereas I have never observed such moss heaths in the interior." The most northerly moss heath is recorded from Marrak ($63^{\circ} 25' N.$). In East Greenland and farther north in West Greenland moss heath does not seem to occur.

Ostenfeld records *Grimmia* heath from the Faeroes (1906, pp. 116). Here it is peculiar to high mountain plateaus and is most abundantly developed in the northern islands. "It is a formation which seems peculiar to an insular and chilly climate" (p. 117).

From the higher regions of the Scottish mountains a *Grimmia* heath of identical appearance and composition is recorded in Tansley's Types of British Vegetation, 1911 p. 211.

In Scandinavia the *Grimmia* heath seems to have been replaced by the Lichen heath.

It holds good of the geographical distribution of the *Grimmia* heath as of its distribution in Iceland that it coincides with the position of the 20% Ch biochore, and is peculiar to areas with abundant rainfall.

The Melar Vegetation. Cf. fig 5 and table 10 A-B.

In the most exposed parts of the *Grimmia* patches the erosion of the wind in the rents of the moss carpet may often be observed. The single stems of the moss are loosened and carried away together with the layer of mould below. The erosion spreads both downwards and round about in the adjacent parts. Its downward action does not stop until the whole surface is paved with the scattered stones dispersed in the layer of mould. In the adjacent parts there is probably no limit to the activity of the erosion. When the mosathembur vegetation has been blown away, the wind works in the same way on the surrounding mo. Consequently large areas of the most exposed parts of Lýngdalsheiði are swept bare of vegetation, especially around Hrólfsheiði and Thrasaborgir. These denuded areas, often termed "fell field" in phytogeographical literature, are called "melar" in Icelandic.

It is peculiar to melar in contrast to other types of vegetation that it is the colour and appearance of the soil rather than the vegetation that determine the physiognomy of the landscape. Ac-

cording to differences with regard to exposure, snow-covering, moisture of the soil, and age of the area, there seem to be differ-

TABLE 10 A. The Melar Vegetation on Lýngdalsheiði.

Localities 1—7 are situated round Hrólfsdalur at about a height of 250 m above sea level. 1—2 examined on ^{12/7} 1925, 3—6 on ^{22/7}, and 7 on ^{5/8} 1925.
(25. $\frac{1}{10}$ m²).

			1	2	3	4	5	6	7
Polygonum viviparum ...	A 3	G	76	84	68	60		80	68
Agrostis canina	E 3	H	60	68	12	8	24	60	88
Salix herbacea	A 3	Ch	24	60	64	16		88	64
Festuca rubra.....	E 4	H	52	40	40	20	36	84	44
— ovina.....	E 4	H	24	64	52	56	20	32	44
Empetrum nigrum	E 4	Ch	2	68	8	2	2	100	92
Juncus trifidus.....	A 2	H	44	56	56	16	4	40	36
Thymus serpyllum	E 4	Ch	20	56	16	4	20	12	76
Luzula spicata	A 2	H	36	36	40	24	24		24
Loiseleuria procumbens..	A 2	Ch	2	28	2	2	2	100	56
Dryas octopetala	A 3	Ch	8	40	20	4	20	20	56
Cerastium alpinum.....	A 3	Ch	36	8	36	24	16		4
Armeria vulgaris.....	A 3	Ch	4	4	52	36	12		16
Silene acaulis	A 3	Ch	16	24	16	12	20		
Arabis petræa	A 1	Ch	8	4	20	20	24		
Cassiope hypnoides.....	A 2	Ch	2	16	8	2	2	32	20
Alchemilla alpina	A 2	Ch	2	2	2	2	2		12
Bartschia alpina	A 2	H	2	2	4	2	2	4	4
Carex rigida	A 3	G	2	4	2	2	2	2	8
Deschampsia alpina	A 2	H	2	2	4	8	2	2	
— flexuosa.....	E 3	H	2	2	2	2	2	8	32
Elyna Bellardi	A 3	H	2	2	2	2	2		20
Equisetum variegatum...	A 3	H	2	2	2	2	2	2	4
Galium boreale	E 2	H	2	2	2	2	2	2	20
— Normanni.....	A 1	H	2	24	2	2	2		64
— verum	E 1	H	2	2	2	2	2	2	8
Luzula arcuata.....	A 3	H	2	2	24	8	2	2	
Pingvicia vulgaris.....	E 4	H	2	2	12	2	2	2	
Poa glauca	A 3	H	4	2	16	2	4	2	2
Rumex acetosa	E 3	H	2	2	4	2	8	2	2
Salix glauca	A 3	Ch	2	2	8	2	2	2	4
Saxifraga hypnoides	A 1	Ch	2	2	2	2	8	2	2
Selaginella selaginoides ..	A 1	Ch	2	2	2	2	2	2	16
Silene maritima	A 1	Ch	2	2	2	2	4	2	2
Tofieldia palustris	A 2	H	2	2	2	2	2	2	12
Trisetum spicatum	A 3	H	2	4	2	2	2	2	20
Vaccinium uliginosum ..	E 4	Ch	2	4	2	2	2	28	24

TABLE 10 B. Biological Spectra of the Melar Vegetation.

	1	2	3	4	5	6	7
Points sum.....	412	692	580	320	220	688	940
Number of species.....	14	20	22	15	13	14	29
Density of species.....	4.1	6.9	5.8	3.2	2.2	6.9	9.4
A	62.1	56.6	75.2	72.5	50.9	52.9	54.5
E	37.9	43.4	24.8	27.5	49.1	47.1	45.5
A 3.....	40.8	32.9	52.4	50.0	23.6	27.3	28.5
A 2.....	19.4	19.7	19.3	15.0	12.7	25.6	17.4
A 1.....	1.9	4.0	3.4	7.5	14.5	»	8.5
E 4.....	23.3	33.5	22.1	25.0	34.5	37.2	29.8
E 3.....	14.6	9.8	2.8	2.5	14.5	9.9	12.8
E 2.....	»	»	»	»	»	»	2.1
E 1.....	»	»	»	»	»	»	0.9
Ch	28.2	45.1	42.8	37.5	45.5	55.2	47.3
H	53.4	42.2	45.5	43.8	54.5	33.1	44.6
G	18.5	12.7	11.7	18.8	»	11.6	8.1
HH	»	»	»	»	»	»	»
Th	»	»	»	»	»	»	»

ences in the vegetation, but owing to the small part played by the vegetation in the appearance of the landscape it is difficult to form an idea as to how much this is the case. It is easiest to ascertain the connection between the vegetation and the age of the area as melar soil. On recently denuded patches hardly any plants are seen, whereas a good deal are seen to have immigrated at a somewhat later stage. Fig. 5 shows such a melar vegetation near Hrólfsheiðar, and table 10 A 1 and 4—5 give the circling results for this and similar localities on Lýngdalsheiði. The density of species is still rather low, 2—4, in spite of the comparatively high number of species, c. 15. Of life forms H and Ch are almost the sole prevailing ones. The most conspicuous species are *Thymus serpyllum*, *Salix herbacea*, *Armeria*, *Silene acaulis*, *Cerastium alpinum*, and *Arabis petraea*; of herbaceous plants *Juncus trifidus*, *Luzula spicata*, *Polygonum viviparum*, *Agrostis canina*, *Festuca ovina*, and *F. rubra* are met with.

On still older stretches of melar not only the vegetation but also the character of the soil have undergone change. The soil

owing to the fact that polygon-formation and solifluction are beginning to be prominent. The vegetation appears changed not only because species already present occur with greater frequency but also because new species have been added. The number of species has almost been doubled, the density has increased from c. 2—4 to c. 6—9. In table 10, 2—3 and 6—7 show the composition of the species on older, more stable tracts of melar. The increase falls especially to Ch. Of new species we may particularly mention *Dryas octopetala*, *Empetrum nigrum*, *Cassiope hypnoides*, *Loiseleuria procumbens*, *Luzula arcuata*, and a number of mo plants. *Dryas octopetala* only occurs in melar on Lýngdalsheiði, not, as is the case in the highlands and the north country, in mo. The presence of *Loiseleuria* and *Cassiope* would seem to show that the localities referred to not only differ from the abovementioned in age but also by being more snow-covered in winter.

On Lýngdalsheiði the melar vegetation is not very widespread, at any rate compared with the mo. In other parts of Iceland, however, it plays a prominent part in the physiognomy of the landscape, not only in the lowlands where it occurs in greatest quantity near the sea, but also and especially in the highlands where the country for miles is covered exclusively with the melar vegetation. At the higher levels it is almost the sole prevailing vegetation.

The melar vegetation or fell field is an arctic type of vegetation and has its greatest distribution north of Iceland, though it occurs at high levels in the Faeroes, Scotland and Scandinavia.

In spite of the great physiognomic differences between the melar and the mosathembur vegetation, the two types must be included in the same class, characterised with regard to environment by not being covered with snow in the winter and biologically by the comparatively great quantity of Ch and A species, especially A 3 species. Both types have their main distribution in arctic regions about, above, or north of the 20 p. c. Ch biocline. The two types show a striking difference in regard to their biological spectra, the melar vegetation having a comparatively high H percentage and a low G percentage, the mosathembur vegetation a high G percentage.

The Mo Vegetation. Figs. 6—7, table 11 A—B.

The mo is the type of vegetation which occupies the largest area of Lýngdalsheiði as well as in the rest of the Icelandic lowlands. The term mo as used here includes all such formations as are normally covered with snow in the winter, whose degree of moisture is exclusively determined by the precipitation, not by the ground water, the soil of which is not in motion, uncultivated, and not covered with forest or copsewood. Thus defined, mo comprises the following of H. Jonsson's formations: heath, heather mo, grass mo, dwarf willow (in part), and grass-field (in part).

The soil of the mo is always more or less covered with knolls as shown in fig. 6. According to the inclination of the surface some differences appear which do not, however, seem to be of great importance in their bearing on the vegetation. Where the surface is level or slightly inclined, the knolls are almost polygonal, half a metre high and broad, and separated from each other by narrow furrows. Where the soil is more inclined, the knolls grow smaller and arrange themselves in longitudinal rows parallel to the edge of the slope. The form of the knoll undergoes a change, not only in that it becomes more elongated, but also because it begins to move downwards. This occurs by a displacement of the material of the knoll itself, apparent by its bulging in the middle of the more or less vertical side facing the valley, and becoming flattened on the upper side. Sometimes the upper side is bare, devoid of vegetation. If all the knolls become flat and bare on the upper side, and outwardly delimited by a vegetation curve, we get typical solifluction, which is especially well developed on mellar in the highland tracts.

If the slope becomes still steeper, the solifluction will assume the character of a landslip. Then it is no longer the single knolls but the substratum that slips, and in consequence the vegetable covering may be preserved intact. Such landslips were observed in the highest stage of development in the highlands and the north country.

Since the mo forms the bulk of the vegetation as a feature of the landscape, it is obvious that forms transitional between the mo and the other types of vegetation must occur. In table 11, Nos. 1—5 represent the typical mo, No. 6 is a transitional form between mo and mosathembur, No. 7 a transitional form between mo and jaðar,

TABLE 11 A. The Mo Vegetation on Lyngdalsheiði.

Localities 1—7 situated in Lyngdalur c. 200 m above sea level. 8 between Hrólfsbólar and Thrasaborgir c. 300 m above sea level (cf. table 13, 9). 9 on Thrasaborgir c. 400 m above sea level (cf. 13, 10). 1—5 and 8—9 represent the typical mo vegetation, 6 a form transitional between mo and mosathembur, 7 a moist mo. 1—6 examined on 28/7 1925, 7 on 29/7 1925, and 8—9 on 23/7 1925. (25. 1/10 m²).

			1	2	3	4	5	6	7	8	9
Salix herbacea.....	A 3	Ch	72	76	72	92	56	68	64	96	96
Empetrum nigrum.....	E 4	Ch	80	80	84	96	100	64	92	36	84
Polygonum viviparum ..	A 3	G	92	64	96	84	92	56	96	80	96
Festuca rubra	E 4	H	92	80	96	100	96	84	92	88	84
Agrostis canina.....	E 3	H	80	84	88	92	100	60	100	100	84
Deschampsia flexuosa..	E 3	H	56	60	72	60	72	16	60	76	52
Carex rigida.....	A 3	G	92	84	88	100	64	84	96	84	80
Juncus trifidus	A 2	H	68	60	48	56	48	20	56	64	20
Luzula spicata.....	A 2	H	32	56	56	60	48	60	48	40	8
Galium boreale	E 2	H	72	60	80	76	76	4	80	92	56
— Normanni	A 1	H	72	68	80	88	76	56	76	84	32
Selaginella selaginoides.	A 1	Ch	52	56	84	88	48	4	80	40	20
Equisetum pratense ...	E 2	G	40	56	96	36	24	40	28
— variegatum.	A 3	H	36	16	12	8	4	16	12	8	48
Thalictrum alpinum ...	A 2	H	36	16	20	44	12	40	64	52	68
Silene acaulis	A 3	Ch	28	32	32	20	16	12	24	20	24
Thymus serpyllum.....	E 4	Ch	24	40	64	60	100	8	16
Cerastium alpinum	A 3	Ch	12	16	..	36	8	32	..	4	..
Trisetum spicatum	A 3	H	20	24	36	60	36	4	28
Festuca ovina	E 4	H	16	28	28	52	56	32	60	4	8
Agrostis tenuis	E 2	H	8	4	4	4	4	4
Cardamine pratensis...	E 4	H	48	24	12	32	12	8	48
Vaccinium uliginosum .	E 4	H	4	..	8	16	44	..	12	..	8
Elyna Bellardi	A 3	H	12	52	28	20
Anthoxanthumodoratum	E 3	H	12	24	..	4	32	..	8
Poa glauca	A 3	H	28	20	8	28	20	20	4
Pingvicia vulgaris	E 4	H	4	..	8	24	4
Galium verum.....	E 1	H	16	16	8	..	8	4
Arctostaphylos uva ursi	E 2	Ch	4
Armeria vulgaris	A 3	Ch	12	..	12	..	4	..
Botrychium Lunaria...	E 4	G	..	8	4
Calluna vulgaris.....	E 2	Ch	4	4
Carex sparsiflora	A 1	G	4	4
Cerastium cæspitosum .	E 3	Ch	4	..
Deschampsia caespitosa.	E 2	H	4	..	4	28
Equisetum arvense	E 4	G	20	..	40	12	..	12
— hiemale ...	E 3	H	8
Euphrasia latifolia....	A 2	Th	4	8	8	4	4

TABLE 11 A. CONTINUED.

		1	2	3	4	5	6	7	8	9
Geranium silvaticum...	E 3	H	>	2	>	4	4	>	>	>
Gnaphalium supinum ..	A 2	Ch	2	2	>	>	>	>	>	8
Habenaria hyperborea .	E 3	G	4	2	>	>	>	>	>	>
Loiseleuria procumbens	A 2	Ch	2	2	>	>	>	>	>	40
Luzula multiflora.....	E 3	H	>	2	>	>	12	>	16	>
Poa alpina	A 2	H	>	2	4	>	>	>	>	>
Potentilla verna	A 2	H	>	2	>	4	>	>	8	>
Ranunculus acer.....	E 4	H	4	2	>	8	4	>	>	4
Rumex acetosa	E 3	H	8	2	4	16	>	12	>	>
Salix glauca	A 3	Ch	>	4	>	4	4	>	>	>
— lanata	A 1	Ch	>	>	>	>	>	>	8	>
— phylicifolia	A 1	Ch	>	>	4	4	16	>	24	>
Taraxacum officinale...	E 2	H	4	>	>	>	>	>	12	>
Tofieldia palustris	A 2	H	2	2	>	4	>	>	>	>
Viola canina	E 3	H	>	16	12	>	>	>	>	>
— palustris	E 3	H	8	>	>	>	8	>	20	>
Viscaria alpina	A 2	H	>	>	4	>	>	>	>	>

TABLE 11 B. Biological Spectra of the Mo-Vegetation.

	1	2	3	4	5	6	7	8	9
Points sum	1240	1232	1344	1524	1304	860	1384	980	944
Number of species ..	35	31	33	38	35	27	32	20	24
Density of species...	12.4	12.3	13.4	15.2	13.0	8.6	13.8	9.8	9.4
A	52.9	52.5	50.3	53.8	41.1	56.7	50.6	58.7	57.6
E	47.1	47.4	49.7	46.2	58.9	43.3	49.4	41.2	42.4
A 3.....	31.6	31.5	27.7	30.4	21.5	35.3	23.4	30.2	36.4
A 2.....	11.0	10.7	10.1	11.5	8.9	14.4	12.7	15.9	15.7
A 1.....	10.3	10.4	12.5	11.8	10.7	7.0	14.5	12.9	5.5
E 4.....	21.9	21.1	22.6	26.8	31.9	27.4	24.0	13.5	20.8
E 3.....	13.5	14.9	13.1	11.5	18.1	10.2	14.7	18.4	14.8
E 2.....	10.3	10.1	13.4	7.9	8.3	5.6	10.7	9.4	6.4
E 1.....	1.3	1.3	0.6	>	0.6	>	>	>	0.4
Ch	22.3	25.0	25.9	28.1	30.4	23.3	23.1	20.8	29.7
H.....	59.0	57.5	52.7	55.6	55.2	50.7	59.2	62.4	50.0
G.....	18.7	17.5	21.1	15.7	13.8	25.6	17.6	16.7	19.9
HH	>	>	>	>	>	>	>	>	>
Th.....	>	>	0.3	0.5	0.6	0.5	>	>	0.4

and finally, 8—9 are the mo vegetation at a somewhat higher level above the sea.

The mo vegetation is very rich in species, in 2.5 sq. m. there occur on an average 35 species of phanerogams or c. 10 p. c. of all Icelandic phanerogams. For the typical mo on Lýngdalsheiði the density of species is 12—15. The biological spectrum shows that H forms the bulk of the vegetation, constituting 50—60 p. c. of all the species noted. The Ch percentage is 25—30, the G percentage 15—2. Th occurs very sparingly. The proportion of the two species groups A and E is as 1 to 1.

As far as the floristic composition is concerned it is difficult to point out one or more species that are physiognomically dominant, and in that respect the knoll formation is most conspicuous.

Of chamaephytes *Salix herbacea* and *Empetrum nigrum* are most important, species such as *Thymus serpyllum*, *Silene acaulis*, and *Cerastium alpinum* being less conspicuous. The other *Salix* species, such as *S. glauca*, *S. lanata*, and *S. phylicifolia* are practically of no consequence, and the same is the case with *Vaccinium uliginosum* — this species occurs principally in mo which adjoins geiri, as shown in table 11, 5. *Calluna vulgaris* and *Arctostaphylos uva ursi* only occur in some few specimens in the mo round Lýngdalur; further down, at the foot of Lýngdalsheiði, both species were physiognomically predominant in the mo, whereas they were only found in the geiri in Lýngdalur. *Loiseleuria procumbens* only occurred sporadically; higher up, at Thrasaborgir, it was considerably more frequent. Of herbaceous plants *Polygonum viviparum*, *Galium boreale*, *G. Normanni* and *Thalictrum alpinum* are most important, a few other species occur more sporadically, particularly *Cardamine pratensis*.

It is, however, grasses or cyperaceous plants that dominate, such as *Festuca rubra*, *F. ovina*, *Agrostis canina*, *Carex rigida*, *Juncus trifidus*, *Elyna Bellardi*, *Luzula spicata*, further *Deschampsia flexuosa*, *Trisetum spicatum*, *Anthoxanthum odoratum*, and *Poa glauca*. Of vascular cryptogams *Selaginella selaginoides*, *Equisetum pratense*, and *E. variegatum* are most frequently met with, while *Botrychium Lunaria* and a few other *Equisetum* species occur now and again.

The typical mo on Lýngdalsheiði is thus characterised by a long series of species, each species occurring with a mean frequency characteristic of the species in question (mean F.-percentage) from which value the individual occurrences deviate but little. In table 11,

1—5 show what species are characteristic of the mo, and the F.-percentage of the individual species. Passing from the mo to one of the vegetation types previously mentioned, a transition zone will often be met with in which the frequencies of the species have undergone great changes. In table 11, 5, 6, and 7 show such transition zones passing into geiri, mosathembur, and jaðar respectively. A comparison of these zones, on the one hand with the mo vegetation, on the other with the respective types of vegetation, will show that statistically, biologically and floristically, the zones occupy this intermediate position.

No. 5 shows the transition from mo to geiri. The geiri plants *Vaccinium uliginosum*, *Luzula multiflora*, and *Anthoxanthum odoratum* show a comparatively high F.-percentage, while a mo plant *Elyna Bellardi* is inconspicuous. The proportion of A and E species points in the same direction. No. 6 is a transitional form between mosathembur and mo. A number of species which occur commonly in the mo, only appear sporadically here: this is the case with *Deschampsia flexuosa*, *Galium boreale*, *Selaginella selaginoides*, *Thymus serpyllum*, and *Trisetum spicatum*. The density of the species is appreciably diminished, being 8.6, and the character of the environment more arctic. The G percentage is comparatively high.

No. 7 is the moist mo which forms the transition to the jaðar vegetation. Most of the plants of the mo recur with the same F.-percentage, a number of jaðar plants such as *Deschampsia cæspitosa*, *Luzula multiflora*, *Salix phylicifolia*, *Viola palustris*, *Cardamine pratensis*, and *Taraxacum officinale* begin to thrive better.

Nos. 8—9 are typical mo at a somewhat higher level, viz. 300—400 m above sea level. The vegetation has assumed a more arctic character. *Salix herbacea* is beginning to predominate in the physiognomy of the vegetation.

As previously indicated, the mo is the most widely distributed type of vegetation in the Icelandic lowland where it probably comprises a fairly large number of formations. It must be left to future plant geographers to classify and characterise these formations with regard to environment, biology, and flora, and to correlate them.

The Jaðar Vegetation.

Between the mo, whose degree of moisture is exclusively determined by the precipitation, and the myri, whose degree of moisture is determined, in addition, by the ground water, there occurs a belt

TABLE 12A. The Vallendi Vegetation on Lýngdalsheiði.

All the localities examined were situated in the upper part of Lýngdalur at the foot of Hrólfsheiði c. 200 m above sea level. 1—2 Salix-vallendi, 3—6 Deschampsia caespitosa-vallendi. 1—2 examined on 10/7 1925, 3—6 on 4-6/7 1925. (25. 1/10 m²).

			1	2	3	4	5	6
Salix lanata	A 1	Ch	72	36	>	>	>	>
— phylicifolia.....	A 1	Ch	60	64	>	>	>	>
Vaccinium uliginosum ...	E 4	Ch	44	12	>	>	>	>
Agrostis tenuis	E 2	H	4	56	100	96	100	96
Festuca rubra.....	E 4	H	96	88	92	96	96	100
Deschampsia caespitosa..	E 2	H	56	28	92	68	88	92
— flexuosa....	E 3	H	>	>	32	48	4	24
Carex rigida	A 3	G	20	24	96	68	68	40
Viola palustris	E 3	H	8	32	92	68	96	76
Galium boreale	E 2	H	44	52	88	88	80	88
Equisetum pratense	E 2	G	52	48	20	>	48	56
Agrostis canina	E 3	H	84	76	28	48	56	4
Polygonum viviparum...	A 3	G	64	68	8	8	56	12
Galium verum	E 1	H	>	12	8	52	4	16
Alchemilla alpina	A 2	Ch	>	4	>	>	>	>
Cardamine pratensis	E 4	H	>	>	12	>	>	20
Empetrum nigrum	E 4	Ch	8	4	>	4	>	>
Equisetum arvense.....	E 4	G	>	>	>	>	20	4
— variegatum ..	A 3	H	>	>	4	8	>	>
Festuca ovina	E 4	H	4	40	>	4	>	8
Galium Normannii.....	A 1	H	>	12	>	4	>	4
Hierochloë odorata	E 2	G	>	>	4	>	8	4
Koenigia islandica.....	A 3	Th	28	>	>	>	>	>
Luzula spicata	A 2	H	4	>	>	>	>	>
Pingvicia vulgaris	E 4	H	4	>	>	>	8	>
Salix glauca	A 3	Ch	>	12	>	>	4	>
— herbacea	A 3	Ch	12	8	>	4	>	>
Selaginella selaginoides ..	A 1	Ch	>	>	>	4	>	4
Taraxacum officinale ...	E 2	H	8	4	4	>	>	4
Thymus serpyllum	E 4	Ch	>	4	>	>	>	>

which is moist in winter, spring, and autumn, but comparatively dry in the vegetation period. On this soil of a medium degree of moisture we meet with a vegetation which is in great part an intermediate form between the mo and the myri vegetation but which, at the same time, comprises a number of specific species. It must be left to future investigators to decide whether there is sufficient

TABLE 12 B.

Biological Spectra of the Valllendi Vegetation.

	1	2	3	4	5	6
Points sum	672	684	680	668	736	652
Number of species	19	21	15	16	15	17
Density of species.....	6.7	6.8	6.8	6.7	7.4	6.5
A	38.7	33.3	15.9	14.4	17.4	9.2
E	61.3	66.7	84.1	85.6	82.6	90.8
A 3.....	18.5	16.4	15.9	13.2	17.4	8.0
A 2	0.6	0.6	»	»	»	»
A 1.....	19.6	16.4	»	1.2	»	1.2
E 4.....	23.2	21.6	15.3	15.6	16.8	20.2
E 3.....	13.7	15.8	22.4	24.6	21.2	16.0
E 2.....	24.4	27.5	45.3	37.7	44.0	52.1
E 1.....	»	1.8	1.2	7.8	0.5	2.5
Ch	29.2	21.1	»	1.8	0.5	0.6
H	46.4	58.5	81.2	86.8	72.3	81.6
G	20.2	20.5	18.8	11.4	27.2	17.8
HH	»	»	»	»	»	»
Th	4.2	»	»	»	»	»

difference between this type, the jaðar vegetation, on the one hand, and the mo and móri vegetations on the other hand, to set it up as a type of the same standing as these. Much would seem to indicate that this is the case. Thus it is a factor of some importance that it appears as a very characteristic feature of the landscape in the highland tracts. *Deschampsia caespitosa*, *Poa pratensis*, and *Agrostis tenuis* are characteristic species on jaðar soil. Types of Icelandic vegetation included herein are valllendi, tún, and móri jaðar. The very remarkable flag vegetation is always associated with it, but owing to very divergent physiognomical, biological, and floristic peculiarities it must be set up as a special type of vegetation.

On Lýngdalsheiði the jaðar vegetation was represented by valllendi and móri jaðar.

The Valllendi Vegetation. Cf. fig. 8 and table 12 A—B.

On the numerous small flat cones deposited by the streams of melting snow, occurring partly in Lýngdalur and partly scattered about throughout the heath, a characteristic vegetation, the valllendi

vegetation, was met with. It is possible to distinguish between two formations, a *Salix lanata* formation on the freshly formed soil, and a *Deschampsia cæspitosa* formation on somewhat older soil. In table 12, 1—6 show the composition of the vegetation in the two formations.

Nos. 1—2 represent the *Salix lanata* vallundi. The soil is only covered with vegetation in patches, the bed of the stream spreading like a net over the surface from the top of the cone, the meshes being filled in with the patches of vegetation. The vegetation is remarkable by the fact that chamaephytes are comparatively dominant physiognomically, especially the two *Salix* species, *Salix lanata* and *S. phyllicifolia*; other Ch occur more sparingly, thus *Vaccinium uliginosum*, *Salix herbacea*, *S. glauca* and *Empetrum nigrum*. Of other plants grasses predominate, especially *Deschampsia cæspitosa*, *Agrostis canina*, and *Festuca rubra*, in less degree *Festuca ovina* and *Agrostis tenuis*. Of other species of more or less importance we may mention *Polygonum viviparum*, *Equisetum pratense*, *Galium boreale*, *Viola palustris*, and *Carex rigida*.

Nos. 3—6 represent the *Deschampsia cæspitosa* vallundi. This formation is always found where the two formations occur together, behind the *Salix* vallundi. The deposition of material has practically ceased here, no bare patches of sand are ever found, and the soil is covered by a dense vegetation of mosses.

The vegetation consists of a luxuriant carpet of hemicryptophytes, principally grasses. Physiognomically *Deschampsia cæspitosa* is the dominant species; in addition *Agrostis tenuis*, *Festuca rubra*, *Deschampsia flexuosa*, *Carex rigida*, and *Agrostis canina* are abundantly represented. Some herbaceous plants occur in the grassy carpet, thus *Galium boreale*, and *Viola palustris*, and less abundantly *Equisetum pratense*, *Polygonum viviparum*, and *Galium verum*.

The two formations occur with the same density of species, c. 7, and from a biological point of view they are remarkable by their large number of southern plants. An essential difference between them is the Ch content. Possibly this difference is due to cultural influences such as grazing or haying.

The Mýri Vegetation, the mýri jaðar and the flói vegetation. From considerations of space and owing to the close agreement between these types in Lýngdalur and at Björk, they will be treated later when the vegetation at Björk is dealt with.

The Geiri Vegetation. Figs. 9—10 and table 13 A—B.

Where for orographic reasons the snow forms a covering early in the autumn, remains on the ground in a more or less deep layer throughout the winter, and does not melt until late spring, a special type of vegetation is developed which may be called by the Icelandic name Geiri (the vegetation of the snow-patches).

It is a characteristic of the snow patch that the underlying soil is never knolly as is the case with the surrounding mo, and further that the vegetation is fairly luxuriant. These two circumstances in conjunction make the snow patch very conspicuous even from a long way off (see figs. 9—10).

In table 13 A the circling results for the geiri vegetation of Lýngdalsheiði have been tabulated; this vegetation is only present in the middle and upper tracts of the heath, from c. 200 m above sea level and upwards. It was most characteristic at the upper levels.

The geiri vegetation comprises several formations which can be distinguished with regard to their environment by differences in the duration and depth of the snow-covering, the height above the sea, and illumination. As regards the general composition of the vegetation the following holds good. *Vaccinium uliginosum* is absolutely the dominant plant, in conjunction with *Empetrum nigrum* and *Deschampsia flexuosa* it forms the bulk of the dense luxuriant carpet of vegetation. Species like *Salix herbacea*, *Calluna vulgaris*, *Agrostis canina*, *Festuca rubra*, *Anthoxanthum odoratum*, *Luzula multiflora*, *Carex rigida*, *Galium boreale*, *G. Normanni*, *Cardamine pratensis*, and *Taraxacum officinale* also abound. *Rubus saxatilis*, *Geranium sylvaticum*, and *Vaccinium myrtillus* are characteristic of the geiri on Lýngdalsheiði. None of these species has been met with in any other type of vegetation. Some typical mo plants occur dispersed throughout the vegetation, in greatest quantity in the least typical snow patches, or in the margin of the larger ones.

In small depressions in the mo, where the snow-covering gives rise to another vegetation than in the mo itself, this vegetation is fairly uniform throughout the depression. In deeper depressions a difference between the vegetation at the bottom and up the sides may be perceived. In table 13 A, 4—5 show respectively the typical geiri vegetation and the vegetation on the sunny northern side of the snow patch. Here the density of species is somewhat greater, 15.5 as against 13.6, owing to a contingent of mo plants.

In still deeper snow patches one may distinguish between a

TABLE 13 A. The Geiri Vegetation on Lýngdalsheiði.

Localities 1—8 situated in Lyngdalur c. 200 m above sea level. 9 between Hrólfsbólar and Thrasaborgir c. 300 m above sea level (cf. table 11, 8). 10 on Thrasaborgir c. 400 m above sea level (cf. table 11, 9). 1 examined on $\frac{2}{7}$ 1925, 2 on $\frac{5}{7}$, 3 on $\frac{8}{7}$, 4—8 on $\frac{10}{7}$, 9—10 on $\frac{23}{7}$ 1925.
 (1—4, 9—10: $25 \frac{1}{10} \text{ m}^2$, 5—8: $10 \frac{1}{10} \text{ m}^2$).

		1	2	3	4	5	6	7	8	9	10
Vaccinium uliginosum...	E 4	Ch	100	100	100	96	100	100	>	>	88
Empetrum nigrum.....	E 4	Ch	100	100	100	80	100	100	90	>	80
Deschampsia flexuosa....	E 3	H	100	100	96	96	100	100	70	100	100
Galium boreale	E 2	H	100	92	84	72	90	70	40	70	68
Salix herbacea	A 3	Ch	68	16	16	76	30	20	80	>	96
Calluna vulgaris	E 2	Ch	40	52	64	28	100	70	100	>	>
Agrostis canina	E 3	H	68	100	76	44	60	80	90	70	100
— tenuis.....	E 2	H	8	>	72	80	30	80	>	100	8
Polygonum viviparum ...	A 3	G	48	8	>	52	60	>	80	>	40
Festuca rubra	E 4	H	56	52	80	80	70	70	70	70	68
Anthoxanthum odoratum	E 3	H	4	52	28	72	100	40	10	>	12
Luzula multiflora	E 3	H	>	20	>	20	40	10	20	>	4
Carex rigida	A 3	G	40	68	64	60	60	30	>	70	84
Galium Normanni.....	A 1	H	32	32	8	36	70	>	40	>	>
— verum	E 1	H	4	16	>	12	50	10	20	>	4
Selaginella selaginoides ..	A 1	Ch	12	8	8	24	20	>	30	>	12
Equisetum pratense	E 2	G	16	16	4	12	40	10	20	10	24
Taraxacum officinale	E 2	H	4	32	12	68	>	20	>	>	12
Geranium sylvaticum....	E 3	H	>	4	4	24	70	>	>	>	12
Vaccinium Myrtillus....	E 2	Ch	>	>	>	88	60	30	>	>	12
Deschampsia cæspitosa ..	E 2	H	>	>	>	12	>	>	>	80	4
Viola palustris	E 3	H	>	>	28	76	>	20	>	100	44
Cardamine pratensis....	E 4	H	36	12	4	32	60	>	>	>	>
Rubus saxatilis	E 3	H	12	4	4	12	>	>	>	>	>
Gnaphalium supinum ...	A 2	Ch	>	>	>	>	>	>	>	>	12
Sibbaldia procumbens ...	A 2	Ch	>	>	>	>	>	>	>	>	44
Alchemilla alpina	A 2	Ch	>	>	>	>	>	>	>	>	16
— minor	E 4	H	>	>	>	24	>	>	>	>	4
Hierochloë odorata	E 2	G	>	8	>	>	>	>	>	>	16
Armeria vulgaris	A 3	Ch	>	>	>	4	>	>	>	>	>
Bartschia alpina	A 2	H	>	>	>	>	>	>	10	>	>
Betula nana	A 2	Ch	>	4	>	2	>	>	>	>	>
Carex sparsiflora	A 1	G	8	8	>	>	>	>	>	>	>
Cassiope hypnoides	A 2	Ch	>	>	>	>	>	>	>	>	4
Elyna Bellardi	A 3	H	>	>	>	>	10	>	10	>	>
Equisetum arvense	E 4	G	>	>	>	4	>	>	>	>	4
— hiemale.....	E 3	H	>	>	4	12	>	>	>	>	4
Eriophorum polystachyum	E 4	G	>	>	>	4	>	>	>	>	4

TABLE 13 A. CONTINUED.

			1	2	3	4	5	6	7	8	9	10
Euphrasia latifolia	A 2	Th	»	»	»	»	»	»	»	»	»	4
Festuca ovina	E 4	H	»	4	»	»	»	»	20	»	»	4
Gnaphalium norvegicum	A 1	H	»	»	»	»	»	»	»	»	»	4
Hieracium sylvaticum....	E 2	H	»	»	»	»	10	»	»	»	»	»
Juncus trifidus.....	A 2	H	8	»	»	»	40	»	20	»	»	»
Leontodon autumnale ...	E 3	H	»	»	»	24	»	»	»	»	4	4
Luzula spicata.....	A 2	H	8	»	»	»	»	»	10	»	»	»
Lycopodium alpinum....	A 2	H	»	»	»	»	»	»	»	»	8	»
Nardus stricta	E 3	H	»	»	»	8	»	»	»	»	»	»
Orchis maculata	E 2	G	»	»	»	8	40	»	10	»	»	»
Pirola minor.....	E 4	H	»	»	»	4	»	»	»	»	»	»
Ranunculus acer	E 4	H	»	»	»	»	»	»	»	»	»	4
Salix glauca.....	A 3	Ch	»	»	»	»	10	»	»	»	»	4
— lanata.....	A 1	Ch	4	»	8	»	»	»	»	»	»	»
— phyllicifolia	A 1	Ch	»	4	4	4	»	»	»	»	»	4
Thalictrum alpinum.....	A 2	H	12	8	»	12	»	»	»	»	12	12
Thymus serpyllum	E 4	Ch	4	8	»	»	80	»	20	»	»	»
Tofieldia palustris.....	A 2	H	»	»	»	»	»	»	10	»	»	»
Trisetum spicatum	A 3	H	»	»	»	»	10	»	»	»	»	»
Viola canina	E 3	H	»	»	»	»	40	»	»	»	»	»

sunny northern margin, No. 7, the typical geiri vegetation chiefly occurring along the sides of the snow patch, No. 6, and the vegetation at the bottom of the snow patch, No. 8. The northern margin is more arctic in character than the typical vegetation. The A percentage is 39.6, while it is only 5.8 for the typical vegetation. The bottom vegetation is almost identical with the previously described *Deschampsia cæspitosa* valllendi both biologically and floristically.

The vegetation of the snow patches at higher levels of Lýngdalsheiði, thus at a height of c. 300—400 m., is shown in table 13 A, 9—10. In its broad features it corresponds to the geiri vegetation at lower levels, though a number of species of common occurrence in the snow patches of Lyngdalur have disappeared, thus *Calluna vulgaris*, *Luzula multiflora*, and several *Galium* species. Others again have become less conspicuous, but on the other hand some new species have been added such as *Gnaphalium supinum*, *G. norvegicum*, *Sibbaldia procumbens*, *Alchemilla alpina*, *A. minor*, *Hierochloë odorata*, and *Veronica alpina*. These species seem to be characteristic of the snow patches in the upper parts of Lýngdalsheiði.

TABLE 13 B. Biological Spectra of the Geiri-Vegetation.

	1	2	3	4	5	6	7	8	9	10
Points sum	892	928	868	1360	1550	860	960	670	960	1104
Number of species	24	27	22	35	27	17	23	9	28	33
Density of species	8.9	9.3	8.7	13.6	15.5	8.6	9.6	6.7	9.6	11.0
A	26.9	16.8	12.4	19.7	20.0	5.8	39.6	10.4	30.0	40.9
E	73.1	83.2	87.6	80.3	80.0	94.2	60.4	89.6	70.0	59.1
A 3	17.5	9.9	9.2	14.1	11.6	5.8	17.7	10.4	22.9	21.0
A 2	3.1	1.3	>	0.9	2.6	>	14.6	>	5.8	15.2
A 1	6.3	5.6	3.2	4.7	5.8	>	7.3	>	1.3	4.7
E 4	33.2	29.7	32.7	23.8	26.5	31.4	20.8	10.4	25.0	17.8
E 3	20.6	30.2	27.6	28.5	26.5	29.1	19.8	40.3	30.0	23.6
E 2	18.8	21.6	27.2	27.1	23.9	32.6	17.7	38.8	15.0	17.4
E 1	0.4	1.7	>	0.9	3.2	1.2	2.1	>	>	0.4
Ch	36.8	31.5	34.6	29.4	32.3	37.2	42.7	>	33.8	34.8
H	50.7	56.9	57.6	60.3	54.8	58.1	45.8	88.1	49.2	48.2
G	12.6	11.6	7.8	10.3	12.9	4.7	11.5	11.9	17.1	16.7
HH	>	>	>	>	>	>	>	>	>	>
Th	>	>	>	>	>	>	>	>	>	0.4

In arctic, Scandinavian, Scottish, and alpine regions these plants are likewise, according to the records, peculiar to places with a deep and persistent snow-covering. The two *Alchemilla* spp. seem to prefer the upper parts of the snow patch, whereas they are absent from the lower parts. — The two snow patch localities correspond to two mo localities, viz. 8—9 in table 11.

Biologically the geiri vegetation is characterised by its low A percentage and high E percentage. The increase in the E percentage is especially due to E 3 and E 2.

B. THE VEGETATION AT BJÖRK.

Above we have described the vegetation in the middle and upper tracts of Lýngdalsheiði, in the following we will subject the vegetation at its foot to further discussion. All investigations of the vegetation were carried out in the vicinity of the Björk farm and with this as their base. It is situated at the foot of Lýngdalsheiði's eastern side at an altitude of c. 100 m.

Some of the types of vegetation recorded from Lýngdalur recur here, viz. mo, jaðar, mýri, and flói, while mellar, mosathembur, and geiri were not developed. In addition there occurred the flag vegetation.

The Mo Vegetation. Cf. table 14 A—B.

In its broad features the appearance and floristic composition of the mo around Björk corresponds to the above-described mo at the higher levels of Lýngdalsheiði.

The soil has the same knolly surface as that previously described, but the knolls are less conspicuous on the slopes than on the flatter parts. The composition of the vegetation is likewise very similar. Almost all the species found in the mo in Lýngdalur recur here and in approximately the same proportions. There are, however, also typical differences partly between this mo and that at the higher levels, and partly between the various parts of the mo around Björk.

Three mo formations could be distinguished, an Elyna mo, an *Arctostaphylos* mo, and a *Calluna-Empetrum* mo. These three formations differ in the following way. The Elyna mo is found on the top of the many little mounds and hills which are covered at the higher levels of Lýngdalsheiði by the mosathembur vegetation, and have a comparatively thin snow-covering. The *Arctostaphylos* mo is found on the sunny slopes of these hills below the Elyna mo, and in the drier depressions among them. The snow-covering is somewhat deeper here and more persistent than in the Elyna mo; it is the normal snow-covering in these parts. Transitional between the *Arctostaphylos* mo and the jaðar is the third mo formation, the *Calluna-Empetrum* mo. Like the *Arctostaphylos* mo, this formation has the normal snow-covering in winter, but differs from the *Arctostaphylos* mo by being more damp. Here the ground water has an appreciable influence on the vegetation. In table 14 A the circling results for these three mo formations have been tabulated.

Plants common to the three mo formations and the mo at higher levels and characteristic of the mo are, e. g. *Empetrum nigrum*, *Thymus serpyllum*, *Salix herbacea*, *Festuca rubra*, *F. ovina*, *Agrostis canina*, *Carex rigida*, *Juncus trifidus*, *Luzula spicata*, *Polygonum viviparum*, *Thalictrum alpinum*, *Selaginella selaginoides*, and *Equisetum variegatum*. Table 14 A shows the proportion in which the various species occur and the good agreement between the

TABLE 14 A.

The Mo Vegetation at Björk.

Localities 1—10 are all situated round Björk c. 100 m above sea level.
 1—4 the Elyna mo., 5—7 the Arctostaphylos mo., 8—10 the Calluna-Empetrum mo. (the moist mo.). 1, 3 and 5 examined on ^{16/7} 1925, 2, 6, 7 and 8 on ^{17/7}, 9 on ^{21/7}, and 4 and 10 on ^{24/7} 1925.
 (25. $\frac{1}{10}$ m²).

			1	2	3	4	5	6	7	8	9	10
Arctostaphylos uva ursi..	E 2	Ch	»	»	4	»	88	96	96	4	4	»
Calluna vulgaris	E 2	Ch	»	12	4	»	76	80	100	96	80	80
Empetrum nigrum	E 4	Ch	100	92	88	80	100	100	100	100	100	100
Thymus serpyllum	E 4	Ch	96	92	76	56	88	92	72	64	80	64
Vaccinium uliginosum...	E 4	Ch	8	12	12	»	88	80	72	68	36	44
Salix herbacea	A 3	Ch	72	60	68	4	80	68	32	28	20	20
Festuca rubra	E 4	H	96	96	100	96	92	100	92	100	100	96
— ovina.....	E 4	H	76	40	8	28	84	80	68	76	60	84
Deschampsia flexuosa....	E 3	H	8	8	40	16	68	52	40	56	36	20
Agrostis canina	E 3	H	88	96	96	100	96	100	92	84	100	88
Carex rigida	A 3	G	76	92	92	80	64	88	60	68	88	76
Polygonum viviparum...	A 3	G	84	72	56	48	68	80	80	100	92	84
Thalictrum alpinum....	A 2	H	32	24	64	36	16	48	64	68	68	60
Galium Normannii.....	A 1	H	88	88	96	80	72	56	32	48	44	68
— boreale	E 2	H	4	48	12	40	84	52	44	28	68	48
Juncus trifidus.....	A 2	H	48	48	36	48	44	36	40	32	76	36
Elyna Bellardi	A 3	H	36	68	48	60	16	4	16	44	64	28
Luzula spicata	A 2	H	64	20	32	32	24	36	52	16	12	28
Selaginella selaginoides ..	A 1	Ch	52	36	32	40	20	28	4	52	48	28
Equisetum pratense	E 2	G	36	16	16	4	20	44	40	60	88	32
— variegatum ..	A 3	H	»	24	24	32	4	32	16	8	12	36
Silene acaulis	A 3	Ch	32	12	16	20	4	12	4	4	8	16
Trisetum spicatum	A 3	H	8	20	8	52	»	20	»	8	24	»
Anthoxanthum odoratum.	E 3	H	»	»	40	4	20	12	4	12	»	»
Luzula multiflora	E 3	H	4	»	16	»	16	4	24	8	8	12
Cardamine pratensis	E 4	H	4	»	12	36	»	»	24	84	52	56
Salix lanata	A 1	Ch	»	4	»	4	12	»	4	28	16	28
— phyllicifolia.....	A 1	Ch	»	»	»	»	»	»	»	28	4	8
Carex sparsiflora	A 1	G	»	»	»	»	8	12	»	40	8	12
Deschampsia caespitosa..	E 2	H	»	»	»	»	»	»	»	12	24	20
Taraxacum officinale	E 2	H	»	»	4	»	4	»	4	20	4	20
Agrostis tenuis.....	E 2	H	»	»	»	»	4	»	»	20	8	28
Equisetum arvense	E 4	G	»	»	»	40	»	»	»	4	12	32
Rumex acetosa	E 3	H	»	»	»	»	»	»	»	8	4	8
Viola palustris	E 3	H	»	»	»	»	»	»	»	8	8	4
Alchemilla alpina	A 2	Ch	»	»	4	»	»	»	»	»	»	»
Armeria vulgaris	A 3	Ch	»	4	»	»	»	»	»	»	»	4
Bartschia alpina	A 2	H	»	»	»	»	»	»	4	»	»	»

TABLE 14 A. CONTINUED.

			1	2	3	4	5	6	7	8	9	10
<i>Botrychium Lunaria</i>	E 4	G	8	>	8	4	>	>	>	4	8	>
<i>Carex rariflora</i>	A 2	G	>	>	>	>	>	>	>	>	4	>
<i>Cerastium alpinum</i>	A 3	Ch	24	>	>	28	>	>	>	4	8	8
<i>Equisetum hiemale</i>	E 3	H	>	>	>	4	>	>	>	>	>	>
<i>Erigeron neglectus</i>	A 1	H	>	>	>	>	>	>	4	>	>	>
<i>Euphrasia latifolia</i>	A 2	Th	>	>	>	>	>	>	>	4	>	>
<i>Galium verum</i>	E 1	H	>	12	32	36	>	>	12	20	4	>
<i>Habenaria viridis</i>	A 1	G	>	>	4	>	>	>	>	>	>	>
<i>Hieracium silvaticum</i>	E 2	H	>	>	>	>	>	>	4	4	>	>
<i>Leontodon autumnale</i> ...	E 3	H	>	>	>	>	>	>	>	>	4	>
<i>Pingvicia vulgaris</i>	E 4	H	>	>	>	>	>	>	4	4	8	>
<i>Poa glauca</i>	A 3	H	>	>	20	8	>	>	>	>	>	4
<i>Potentilla verna</i>	A 2	H	4	>	>	4	>	>	>	>	4	16
<i>Ranunculus acer</i>	E 4	H	>	>	>	>	>	>	>	4	>	>
<i>Rhinanthus minor</i>	E 2	Th	>	>	>	>	>	8	>	>	>	>
<i>Salix glauca</i>	A 3	Ch	>	>	>	4	>	>	>	>	>	>
<i>Viola canina</i>	E 3	H	>	>	>	>	8	>	>	12	>	>

TABLE 14 B. Biological Spectra of the Mo-Vegetation.

	1	2	3	4	5	6	7	8	9	10
Points sum	1148	1096	1168	1124	1368	1424	1304	1532	1508	1396
Number of species.	25	25	32	31	29	28	32	41	42	36
Density of species.	11.5	11.0	11.7	11.2	13.7	14.2	13.0	15.3	15.1	14.0
A	54.0	52.2	51.4	51.6	31.6	36.5	31.6	37.9	39.8	40.1
E	46.0	47.8	48.6	48.4	68.4	63.5	68.4	62.1	60.2	59.9
A 3.....	28.9	32.1	28.4	29.9	17.3	21.3	16.0	17.2	21.0	19.8
A 2.....	12.9	8.4	11.6	10.7	6.1	8.4	12.3	7.8	10.9	10.0
A 1.....	12.2	11.7	11.3	11.0	8.2	6.7	3.4	12.8	8.0	10.3
E 4.....	33.8	30.3	26.0	30.2	33.0	32.0	33.1	33.4	30.2	34.1
E 3.....	8.7	9.5	16.4	11.0	15.2	11.8	12.3	11.5	11.4	9.5
E 2.....	3.5	6.9	3.4	3.9	20.2	19.7	22.1	15.9	18.3	16.3
E 1.....	>	1.1	2.7	3.2	>	>	0.9	1.3	0.3	>
Ch	33.4	29.6	26.0	21.0	40.6	39.0	37.1	31.1	26.8	28.7
H	48.8	54.0	58.9	63.3	47.7	44.7	49.1	50.7	53.3	54.4
G	17.8	16.4	15.1	15.7	11.7	15.7	13.8	18.0	19.9	16.9
HH	>	>	>	>	>	>	>	>	>	>
Th	>	>	>	>	>	0.6	>	0.3	>	>

species in the three formations; if compared with table 11, it will further show the agreement between the mo at Björk and that of Lýngdalur.

The Elyna Mo. Table 14 A, 1—4. The dominant here is *Elyna Bellardi*. It occurs especially at the top of the knolls and with its brown, tufted stems it contributes markedly to the peculiar physiognomy of the vegetation. Other characteristic plants are *Silene acaulis*, *Cerastium alpinum*, *Trisetum spicatum*, and *Poa glauca*. These species attain their finest development here even though they are also found in the other formations. Further it is characteristic of the Elyna mo that a number of species otherwise always present in the mo are rare or absent here, viz. *Vaccinium uliginosum*, *Calluna vulgaris*, *Arctostaphylos uva ursi*, *Deschampsia flexuosa*, *Galium boreale*, and *Luzula multiflora*. All these plants are southern species.

The Arctostaphylos mo. Table 14 A, 5—7. Physiognomically characteristic of this formation are above all *Arctostaphylos uva ursi*, *Calluna vulgaris*, and *Vaccinium uliginosum*; further there occur *Deschampsia flexuosa*, *Galium boreale*, *Luzula multiflora*, and *Anthoxanthum odoratum*. On the other hand, *Elyna Bellardi*, *Selaginella selaginoides*, *Silene acaulis*, *Cerastium alpinum*, *Trisetum spicatum*, and *Poa glauca* are not dominant, a feature by which this formation differs from the Elyna mo. The difference between the two mo formations thus consists in the fact that the Elyna mo has many arctic but comparatively few southern species in contrast to the Arctostaphylos mo in which the southern species are dominant. This difference is decidedly due to the difference in the snow-covering. From both formations the species requiring moisture, which occur in the Empetrum mo, are absent.

The Calluna-Empetrum Mo. As mentioned above, this formation occurs as a narrow border between the Arctostaphylos mo and the jaðar, and it is particularly well developed where the ground is slightly inclined. The most striking difference between this and the above-mentioned formation is the absence of *Arctostaphylos uva ursi*. Owing to the immediate vicinity of the jaðar some of the plants characteristic of that formation are met with, though sporadically, thus *Carex sparsiflora*, *Cardamine pratensis*, *Deschampsia cæpitosa*, *Taraxacum officinale*, *Agrostis tenuis*, *Equisetum arvense*, *Viola palustris*, *Salix lanata*, and *S. phylicifolia*.

The situation of these two formations in relation to each other affords an excellent illustration of the relation to moisture of *Arctostaphylos uva ursi* and *Calluna vulgaris*. On the heath of Jutland we may similarly distinguish between a higher tract with *Arctostaphylos* and *Calluna* and a lower tract where *Arctostaphylos* is absent. Though the environment differs widely in the Icelandic mo and the heath of Jutland, it is worth noting that species which they have in common react similarly to the same change of environment. It is not the sum of environmental factors but the individual factors of the environment which determine the distribution of the species.

The Jaðar and Mýri Vegetations: Fig. 11 and table 15 A—B.

In areas where the degree of moisture is determined both by the precipitation and the ground water we meet with those stretches which are called "mýrar" in Icelandic. Owing to the abundant precipitation the mýri is very extensively distributed throughout the Icelandic lowlands. Several types of mýri are found. Of most common occurrence is the »fórmýri« or swampy mýri, formed in cup-shaped depressions on level or slightly inclined ground. Its formation and peculiarities are due to the sour stagnant ground water. Where the soil grows very damp, that is to say, where the ground water covers the bottom all the year round, swampy stretches, "floar" are formed. The second type of mýri is the »hallamýri« or well mýri. This is formed where the ground water is pressed up out of the soil, hence it is often seen at the foot of mountains. Where the water is pressed up with such force that springs are formed and where the bottom is therefore swampy and damp all the year round the "dý" vegetation is formed.

The third type of mýri is the "fétmýri" or irrigated mýri formed on tracts inundated by water for shorter or longer periods of the year. Natural fétmýrar are thus formed on the banks of rivers but most extensively in deltas near the sea. The characteristic plant in this type of mýri is *Carex Lyngbyei*, and since this plant is an important forage plant, successful damming experiments have lately been made with a view to creating conditions for an inundation mýri in places where it was not formerly found.

Three different types of vegetation are associated with these three types of mýri. I was afforded most opportunity for a thorough-going study of the swampy mýri which I investigated both in Lyng-

dalur, at Björk, and at Lækjamót in the north country. The ridge mýri I have only investigated at Lækjamót, while I had no opportunity of a close study of the fétmýri.

The composition of the swampy mýri in Lyngdalur and at Björk is shown in table 15 A, 1—11.

Fig. 11 shows the appearance of the mýri at Björk. The soil is markedly knolly, but the knolls are smaller and more scattered than on the mo.

According to the degree of moisture of the soil it is possible to distinguish between the following formations. The mýri jaðar (the margin of the mýri) or the grass mýri is first met with on passing from the mo on to the mýri. Upwards it passes into the moist mo, the *Calluna-Empetrum* mo. The ground water hardly ever comes up to the surface, but the bottom is damp in spring, winter, and autumn, whereas, in the vegetation period, it is comparatively dry. Outwards the jaðar passes into the dry cyperaceous mýri, the *Salix* mýri. The soil is here considerably more moist, in wet summers the water will perhaps cover the surface throughout the vegetation period; normally, however, this vegetation will not be covered with surface water the greater part of the vegetation period, in dry summers perhaps not at all. On the dampest soil we find the moist cyperaceous mýri or the *Betula nana* mýri. The bottom must here be assumed to be covered with water even in normal summers; in very dry summers dry bottom may no doubt be found in this formation, too. The flói, or swamp, is met with in spots in this formation. Here the bottom is always covered with water, even in dry summers. The knolls, so typical of the mýri, are not present in the flói, and while the soil of the mýri is firm to the tread, rendered solid by a dense web of Cyperaceae rhizomes, the ground in the flói is soft and muddy, and one moves on it in constant fear of sinking into the slush.

On a gentle slope these 4 belts will succeed each other in the sequence described above, adjoining the moist mo upwards, while outwards they will perhaps be succeeded by a collection of water, a "tjörn" (tarn). Where the surface is more irregular, a comparatively moist formation will not rarely adjoin a comparatively dry one, while the intermediate formations are not developed.

The Jaðar Vegetation. Table 15 A, 1—3 shows the floristic composition of this vegetation in Lyngdalur and at Björk. The

number of species and density are comparatively high, on an average c. 40 species in 25 sq. m. with a density of c. 14. The southern species play a much greater part than the arctic species; of the life forms H predominate with an average percentage amount of more than 50. Ch attain their minimum here; both above and below they constitute a larger percentage amount of the vegetation than here. The G percentage is somewhat higher than in the mo.

With regard to the floristic composition, we find not only a number of species from the mo, such as *Empetrum nigrum*, *Vaccinium uliginosum*, *Salix herbacea*, *Polygonum viviparum*, *Thalictrum alpinum*, *Agrostis canina*, *Festuca rubra*, *F. ovina*, and *Carex rigida*, but also a number of species which must be said to be peculiar to the jaðar. Of these *Deschampsia cæspitosa*, the typical dominant for the jaðar, must especially be noted, even though its F.-percentage is not always very high. Further *Agrostis tenuis*, *Carex sparsiflora*, *C. capitata*, *Taraxacum officinale*, *Cardamine pratensis*, and *Viola palustris*, as also the *Salix* species, *S. phylicifolia* and *S. lanata*. Most of these species attain their maximum development here. Of plants peculiar to the myrì *Carex Goodenoughii* is the only one which plays any great part in the jaðar vegetation.

The *Salix* Myrì. Table 15 A—B, 4—6.

Similarly to the jaðar this formation has a large average number of species and high average density, though not as high as in the jaðar. While grasses were dominant in the jaðar here it is the Cyperaceae, and the result is a great decrease in the H percentage and a corresponding increase of the G percentage in the biological spectrum. HH are gradually gaining ground and are represented by c. 6—8 p. c. in the spectrum. The Ch percentage is somewhat higher than in the jaðar. The proportion of A and E species is practically the same for this and the above-mentioned formation, but there is a displacement within the subgroups. The E 2 percentage is comparatively high in the former, considerably lower in the latter formation.

Floristically the *Salix* myrì differs from the jaðar in that the grasses play a very slight part, while the *Salix* species are the same. From the *Betula nana* myrì it is distinct by the absence of the characteristic species of that formation, *Betula nana*, but it has the same cyperaceous flora. The dominant species are *Garex Goodenoughii*, *Eriophorum polystachyum* and the *Salix* spp. especially

TABLE 15 A.

The Jaðar and Mýri Vegetation on Lýngdalsheiði and at Björk.

Localities 1—3 represent the Jaðar vegetation. No. 1 in Lýngdalur c. 200 m above sea level. 2—3 at Björk c. 100 m above sea level. 4—6 the *Salix myri*, 4—5 at Björk, 6 in Lýngdalur. 7—11 the *Betula nana* myri, 7—9 in Lýngdalur, 10—11 at Björk. 9 examined on 4/7 1925, 2 and 11 on 18/7, 5 on 20/7, 4 on 21/7, 1, 6, 7 and 8 on 22/7, and 10 on 25/7 1925.
(25. $\frac{1}{10}$ m²).

		1	2	3	4	5	6	7	8	9	10	11
Deschampsia caespitosa.	E 2	H	64	44	72	12	>	4	>	2	2	2
Calamagrostis neglecta .	E 4	H	56	8	44	>	>	>	8	>	2	2
Agrostis tenuis	E 2	H	96	44	4	4	4	>	2	2	2	2
Carex rigida	A 3	G	100	28	56	4	8	60	>	52	48	2
Cardamine pratensis...	E 4	H	48	60	80	60	20	24	4	>	8	16
Agrostis canina.....	E 3	H	72	32	48	32	32	28	>	4	2	2
Viola palustris	E 3	H	36	68	28	88	64	44	>	>	2	2
Festuca rubra	E 4	H	96	96	100	88	80	92	12	32	32	4
— ovina	E 4	H	72	80	68	96	48	44	>	12	2	20
Salix phylicifolia	A 1	Ch	88	32	8	20	32	72	40	12	16	24
— lanata	A 1	Ch	>	52	52	76	60	8	>	>	2	4
— herbacea	A 3	Ch	20	60	12	28	56	48	16	24	4	16
Equisetum arvense	E 4	G	48	60	20	20	56	16	>	>	2	2
Polygonum viviparum..	A 3	G	96	92	92	96	92	92	92	92	96	88
Thalictrum alpinum ...	A 2	H	96	80	80	40	84	80	12	64	68	>
Comarum palustre	E 4	HH	12	28	4	76	72	56	16	>	28	40
Carex Goodenoughii ...	E 3	G	88	76	32	100	100	100	96	96	100	100
— rariflora.....	A 2	G	28	4	>	88	52	88	88	92	92	44
— chordorrhiza	A 1	G	>	12	>	12	72	4	88	96	100	100
— rostrata	E 3	HH	>	8	>	8	32	4	8	36	76	44
Eriophorum polysta-												
— chyrum	E 4	G	48	28	8	96	76	68	88	52	72	100
Empetrum nigrum....	E 4	Ch	28	88	56	76	96	24	48	84	52	92
Vaccinium uliginosum .	E 4	Ch	4	92	40	56	100	24	76	100	100	100
Bétula nana.....	A 2	Ch	>	>	>	12	16	8	24	84	100	100
Carex sparsiflora	A 1	G	12	16	20	>	>	>	>	2	2	2
— capitata	A 2	H	4	4	16	>	>	>	>	2	2	2
Taraxacum officinale ..	E 2	H	>	24	20	>	8	>	>	2	2	2
Luzula multiflora.....	E 3	H	16	8	12	4	8	>	>	2	2	2
Equisetum pratense....	E 2	G	8	8	28	>	>	>	>	2	2	2
— variegatum	A 3	H	40	12	24	36	20	8	>	2	2	2
Galium Normanni	A 1	H	24	36	48	12	4	12	>	2	2	2
— boreale	E 2	H	40	20	28	4	20	16	>	2	2	12
Potentilla verna	A 2	H	12	8	16	4	12	>	4	>	2	2
Selaginella selaginoides.	A 1	Ch	20	28	40	16	8	4	>	4	4	8
Salix glauca	A 3	Ch	8	20	4	8	36	12	16	>	20	4

TABLE 15 A CONTINUED.

			1	2	3	4	5	6	7	8	9	10	11
Pingvicia vulgaris	E 4	H	»	»	»	4	4	»	4	8	8	»	16
Scirpus caespitosus	E 4	H	»	»	»	»	»	»	20	40	40	»	8
Menyanthes trifoliata....	E 4	HH	»	»	»	20	»	»	»	12	»	20	36
Agrostis alba	E 3	H	»	»	4	20	»	»	»	»	»	»	»
Calluna vulgaris	E 2	Ch	»	12	»	»	»	»	»	»	»	»	»
Carex alpina	A 2	H	12	»	»	»	»	»	»	»	»	»	»
— canescens	E 4	H	»	»	»	16	»	»	4	»	»	»	»
— dioica.....	E 4	G	4	»	»	»	»	4	4	»	»	»	»
— limosa.....	E 2	G	»	»	»	»	»	»	»	»	»	»	20
— panicea.....	E 3	G	»	»	24	»	»	»	»	»	»	»	4
Deschampsia alpina....	A 2	H	4	»	»	»	»	»	»	»	»	»	»
— flexuosa	E 3	H	»	4	12	»	»	»	»	»	»	»	»
Elyna Bellardi.....	A 3	H	»	»	8	»	»	»	»	»	»	»	»
Equisetum limosum ...	E 2	HH	»	»	»	»	4	»	»	»	»	12	16
Eriophorum Scheuchzeri	A 3	HH	»	»	»	8	»	4	»	8	»	»	8
Euphrasia latifolia.....	A 2	Th	»	»	»	»	»	4	»	»	»	»	»
Galium verum.....	E 1	H	»	»	8	»	»	»	»	»	»	»	»
Geum rivale	E 2	H	»	»	»	»	»	8	»	»	»	»	4
Hierochloë odorata.....	E 2	G	40	8	»	»	16	8	»	»	»	»	»
Juncus balticus.....	A 1	G	»	»	»	»	4	»	»	»	»	»	»
— filiformis	E 3	G	»	»	4	4	»	»	»	»	»	»	»
— trifidus	A 2	H	4	»	12	»	»	»	»	»	»	»	»
Leontodon autumnalis..	E 3	H	»	4	»	»	»	»	»	»	»	»	»
Luzula spicata	A 2	H	»	»	4	»	»	»	»	»	4	»	»
Poa alpina	A 2	H	8	»	»	»	»	»	»	»	»	»	»
— pratensis.....	E 4	G	»	8	»	8	»	»	»	»	»	»	»
Ranunculus acer.....	E 4	H	»	»	»	»	4	»	»	»	»	»	»
Rhinanthus minor.....	E 2	Th	4	4	»	»	»	»	»	»	»	»	»
Rumex acetosa	E 3	H	»	»	4	»	»	»	»	»	»	»	»
Spiraea ulmaria	E 2	H	»	»	»	8	»	4	»	»	»	»	4
Thymus serpyllum.....	E 4	Ch	»	4	16	»	»	»	»	»	»	»	»
Tofieldia palustris	A 2	H	»	»	»	»	»	»	»	»	»	»	»
Triglochin palustre ...	E 4	H	»	»	»	»	4	»	»	»	»	»	»
Trisetum spicatum	A 3	H	12	4	»	»	4	4	»	»	4	»	4
Viola canina	E 3	H	»	»	4	»	»	»	»	»	»	»	»

S. lanata. The species common to this formation and those above, and which are not present or only occur sporadically in the moist *Betula nana* myri are the following. *Salix herbacea*, *S. lanata*, *Viola palustris*, *Cardamine pratensis*, *Agrostis canina*, *Festuca rubra* and *F. ovina*, and *Equisetum arvense*. The following species are

TABLE 15 B.

Biological Spectra of the Jaðar- and Mýri Vegetation.

	1	2	3	4	5	6	7	8	9	10	11
Points sum	1376	1404	1352	1360	1408	1076	752	1004	1076	888	1032
Number of species	38	42	42	39	38	34	19	21	23	16	35
Density of species	13.8	14.0	13.5	13.6	14.1	10.8	7.5	10.0	10.8	8.9	10.3
A	42.7	34.8	36.4	33.8	39.8	47.2	50.0	52.6	51.7	40.5	40.7
E	57.3	65.2	63.6	66.2	60.2	52.8	50.0	47.4	48.3	59.5	59.3
A 3	20.1	15.4	14.5	13.2	15.3	21.2	16.5	17.5	16.0	10.4	10.1
A 2	12.2	6.8	9.5	10.6	11.6	16.7	16.5	23.9	24.5	16.2	18.2
A 1	10.5	12.5	12.4	10.0	12.8	9.3	17.0	11.2	11.2	14.0	12.4
E 4	30.2	39.3	32.2	45.3	39.8	32.7	36.2	33.9	32.0	41.9	39.9
E 3	15.4	14.2	12.7	18.8	16.8	16.4	13.8	13.5	16.4	16.2	14.0
E 2	11.6	11.7	18.0	2.1	3.6	3.7	>	>	>	1.4	5.4
E 1	>	>	0.6	>	>	>	>	>	>	>	>
Ch	12.2	27.6	16.9	21.5	28.7	18.6	29.3	30.7	27.5	36.0	29.5
H	52.9	45.3	61.8	38.8	29.8	34.2	7.4	15.9	15.2	2.3	15.9
G	33.7	24.2	21.0	31.5	33.8	40.9	60.1	47.8	47.6	48.6	41.9
HH	0.9	2.6	0.3	8.2	7.7	5.9	3.2	5.6	9.7	13.1	12.8
Th	0.3	0.3	>	>	>	0.4	>	>	>	>	>

common to the dry and the \pm moist Cyperaceae mýri. *Carex Goodeoughii*, *C. chordorrhiza*, and *C. rariflora*, besides *Eriophorum polystachyum*. Common to all three formations are *Empetrum nigrum*, *Vaccinium uliginosum*, *Salix phyllicifolia*, *Polygonum viviparum*, and *Thalictrum alpinum*.

The Betula nana Mýri. Table 15 A—B, 7—11.

In this formation the change from jaðar to Salix mýri has progressed still further. The number and density of the species is appreciably diminished. H have decreased considerably and G have attained a maximum. The Ch and HH percentages have also risen. The species group spectrum has likewise undergone a change. The quantity of A species has increased somewhat, and in the A subgroups there is displacement from A 3 to A 2 and A 1. The E subgroups show a displacement in the direction of E 4.

Physiognomically chamaephytes and Cyperaceae are dominant, thus of chamaephytes especially *Betula nana*, *Vaccinium uliginosum*,

and *Empetrum nigrum*, and in less degree *Salix phylicifolia*. Of Cyperaceae *Carex Goodenoughii*, *C. chordorrhiza*, *C. rariflora*, and *Eriophorum polystachyum* are particularly conspicuous. To these must be added *Polygonum viviparum* and *Thalictrum alpinum*. Of the marsh plants *Carex rostrata* is the most important. *Comarum palustre*, *Menyanthes trifoliata* and *Equisetum limosum* occur more sporadically.

The Flói Vegetation. Table 16 A—B, 1—5.

The vegetation is not evenly distributed over the surface of the myri; a number of the species, especially the chamaephytes, are peculiar to the knolls, others, the Cyperaceae, only occur in the spaces between the knolls. Passing from the myri towards the flói, the spaces between the knolls grow larger and larger until the knolls have quite disappeared and with them their vegetation.

In table 16 A—B are tabulated the circling results for all the lowland localities investigated in Iceland, from Lýngdalsheiði, Björk and Lækjamót. The reason why so few localities were investigated was that the rainy summer of 1925 afforded very poor working conditions. In spite of the few localities, the table gives interesting and mutually agreeing particulars of the flói vegetation. Compared with the myri vegetation it is very poor in species, the number of species being 2—4, the density 1—2. Geophytes and helophytic Cyperaceae form the bulk of the vegetation, thus especially *Eriophorum polystachyum*, *Carex Goodenoughii*, *C. chordorrhiza* and *C. rostrata*. A few other species occur sporadically.

The greatest interest attaches to the biological conditions when compared with those of the myri vegetation. The species group spectrum shows a strong concentration in the central part of the spectrum from E 3 to A 1; the lower groups, and in part the upper ones, are not represented in the spectrum.

This spectrum seems to be typical of vegetations on a water-covered surface. The Subularia flag, whose vegetation is covered by a water layer as deep as that of the flói, has practically the same species group spectrum as the flói with a large predominance in the central part of the spectrum. The same is the case with the highland flói.

The statistical and biological conditions of the flói are, as a comparison of the respective tables will show, a further development

TABLE 16 A-B.

The Flói Vegetation in Lyngdalur, at Björk, and at Lækjamót.

1—2 situated in Lyngdalur, 3—4 at Björk, and 5 at the bottom of the valley at Lækjamót. 1—2 examined on $^{22}/7$ 1925, 3—4 on $^{27}/7$ 1925, and 5 on $^{21}/8$ 1925.

			1	2	3	4	5
Carex Goodenoughii.....	E 3	G	36	100	32	100	»
— chordorrhiza.....	A 1	G	»	4	»	100	100
Eriophorum polystachyum..	E 4	G	»	»	4	20	100
Carex rostrata.....	E 3	HH	»	»	100	»	»
Ranunculus reptans.....	E 4	H	88	»	»	»	»
Carex rariflora.....	A 2	G	»	»	»	12	»
— saxatilis.....	A 3	G	»	»	»	»	4
Comarum palustre.....	E 4	HH	»	»	4	»	»
Menyanthes trifoliata.....	E 4	HH	»	»	4	»	»
Number of species.....	Flag-vegetation ¹		2	2	5	4	3
Density of species.....			1.2	1.0	1.4	2.3	2.0
A.....	»	28.2	»	3.8	»	48.3	51.0
E.....	100	71.8	100.0	96.2	100.0	51.7	49.0
A 3.....	»	28.2	»	»	»	»	2.0
A 2.....	»	»	»	»	»	5.2	»
A 1.....	»	»	»	3.8	»	43.1	49.0
E 4.....	23.3	18.4	71.0	»	8.3	8.6	49.0
E 3.....	76.7	53.5	29.0	96.2	91.7	43.1	»
E 2.....	»	»	»	»	»	»	»
E 1.....	»	»	»	»	»	»	»
H.....	10.0	11.2	71.0	»	»	»	»
G.....	23.3	12.7	29.0	100.0	25	100.0	100.0
HH.....	»	»	»	»	75	»	»
Th.....	66.7	76.1	»	»	»	»	»

of the changes occurring in the myri formations from the comparatively dry to the comparatively wet formations.

The Flag Vegetation: Cf. figs. 12—13 and table 17 A—B.

On the border line between mo and myri are often found long narrow strips of land called "flag" in Icelandic. In a floristic and physiognomic respect the flag deviates much from the surrounding mo or myri, and by its mixture of pronounced arctic (A 3) and

¹ Cf. table 17 B 1—2.

pronounced southern (Th) types of plants it is one of the most remarkable and interesting vegetations of Iceland.

The flag occurs as from 2—3 to 15—20 m. wide and often very long clayey flats delimited upwards towards the mo by a more or less connected slope and outwards towards the myri by a connected ridge (cf. figs. 11—12). The soil of the flag is level and horizontal. If covered with water the whole of the summer it is a naked clayey flat without any trace of knolls. If such a flat is laid dry, the familiar polygonal cracks appear. If the soil is not covered with water in the summer, it will always be cracked, and a greater or smaller number of small knolls covered with vegetation will be spread over the surface. Such is the typical appearance of the flag. If the soil grows drier still, the knolls increase in number as well as in size and we get the flag mo, though the bare clay surface still predominates.

The flag vegetation seems to comprise a number of formations. Table 17 A shows the circling results for three such formations, the Subularia flag, the Koenigia flag, and the flag mo.

The Subularia flag was examined in a single locality, the myri at Björk. Here a long strip of Koenigia flag occurred in connection with a small brook. The Subularia flag was found at the transition from the Koenigia flag to the brook. At the time when the investigation was made, (the close of July), the soil was covered with water. In the deepest water only scattered specimens of *Subularia aquatica* were found (table 17 A, 1), while further in (table 17 A, 2) it was found in company with some other species such as *Koenigia islandica*, *Juncus bufonius*, *Equisetum arvense*.

From East Iceland a formation has been recorded by Helgi Jónsson which must probably be referred to the flag. "Where the soil has an admixture of clay little pools are formed in the depressions which evaporate in the course of the summer. In these places the vegetation varies not a little, consisting now almost exclusively of *Subularia aquatica*, now on the other hand only of *Ranunculus reptans* which colours such spots quite yellow. I have seen both species occur in such quantities that they coloured the whole bottom of the pool white or yellow. In other places I saw that the vegetation consisted of *Ranunculus reptans*, *Subularia aquatica*, *Alopecurus fulvus* and *Juncus supinus* fairly equally distributed, so that neither one nor the other could be designated as the characteristic plant."

TABLE 17 A.

The Flag Vegetation at Björk and Lækjamót.

Localities 1—5 situated in South Iceland at Björk c. 100 m above sea level. 1—2 Subularia flag; 3—5 Koenigia flag; 6—7 flag mo from North Iceland, Lækjamót, c. 50 m above sea level. 1, 2, and 5 examined on 25/7 1925, 3 on 18/7, and 4 on 21/7 1925; 6—7 on 20/8 1925. (25. 1/10 m²).

		1	2	3	4	5	6	7
Subularia aquatica	E 3	Th	80	76	0	0	0	0
Koenigia islandica	A 3	Th	0	80	100	100	100	100
Juncus bufonius	E 3	Th	0	60	76	96	64	0
Sedum villosum	A 2	H	0	0	96	100	100	88
Agrostis alba	E 3	H	12	16	92	100	96	96
Juncus triglumis	A 3	H	0	0	76	68	36	64
— biglumis.....	A 3	H	0	0	48	36	36	48
Triglochin palustre.....	E 4	H	0	16	88	68	68	68
Polygonum viviparum	A 3	G	0	0	72	76	76	88
Equisetum arvense	E 4	G	28	36	44	48	36	52
Sagina nodosa	E 3	H	0	0	48	60	24	52
Festuca ovina.....	E 4	H	0	0	28	36	20	36
Deschampsia alpina	A 2	H	0	0	8	40	4	28
Luzula spicata	A 2	H	0	0	24	12	48	72
Minuartia verna.....	A 3	Ch	0	0	20	36	12	0
Cerastium caespitosum ...	E 3	Ch	0	0	24	60	0	88
— alpinum.....	A 3	Ch	0	0	0	0	48	48
Silene acaulis	A 3	Ch	0	0	0	0	0	20
Armeria vulgaris	A 3	Ch	0	0	0	0	0	24
Rumex acetosa.....	E 3	H	0	0	0	0	0	40
Poa alpina.....	A 2	H	0	0	0	0	0	28
— glauca	A 3	H	0	0	0	0	0	4
Thalictrum alpinum.....	A 2	H	0	0	0	0	0	28
Parnassia palustris	E 2	H	0	0	0	0	0	28
Carex capillaris	A 3	H	0	0	0	0	0	20
Pingvicia vulgaris	E 4	H	0	0	0	0	0	4
Agrostis tenuis.....	E 2	H	0	0	0	0	0	8
Arenaria ciliata	A 3	Ch	0	0	0	0	0	20
Cardamine pratensis	E 4	H	0	0	8	0	0	0
Draba incana	A 2	H	0	0	0	0	0	8
Empetrum nigrum	E 4	Ch	0	0	4	4	0	4
Epilobium alsinifolium ..	A 1	H	0	0	0	0	0	0
Equisetum pratense	E 2	G	0	0	4	0	0	0
Euphrasia latifolia	A 2	Th	0	0	0	0	0	0
Festuca rubra.....	E 4	H	0	0	0	0	24	4

TABLE 17 A. CONTINUED.

		1	2	3	4	5	6	7
Juncus trifidus.....	A 2	H	»	»	»	»	»	8
Leontodon autumnalis...	E 3	H	»	»	»	»	8	»
Linum catharticum	E 1	Th	»	»	»	8	»	»
Potentilla verna.....	A 2	H	»	»	»	»	4	»
Rhinanthus minor.....	E 2	Th	»	»	»	»	»	»
Salix herbacea	A 3	Ch	»	»	16	»	»	»
Saxifraga oppositifolia ...	A 3	Ch	»	»	»	»	»	4
Spergula arvensis	E 2	Th	»	»	»	8	»	»
Taraxacum officinale	E 2	H	»	»	»	»	»	4
Thymus serpyllum	E 4	Ch	»	»	»	»	4	»
Viola palustris.....	E 3	H	»	»	4	»	»	»

TABLE 17 B. Biological Spectra of the Flag Vegetation.

	1	2	3	4	5	6	7
Points sum.....	120	284	884	960	812	1156	1040
Number of species	3	6	21	19	20	29	29
Density of species.....	1.2	2.8	8.8	9.6	8.1	11.6	10.4
A	»	28.2	52.5	49.2	56.7	58.1	68.5
E	100.0	71.8	47.5	50.8	43.3	41.9	31.5
A 3.....	»	28.2	37.6	32.9	37.9	36.0	46.9
A 2.....	»	»	14.9	15.8	18.7	22.1	21.5
A 1.....	»	»	»	0.4	»	»	»
E 4.....	23.3	18.4	19.5	16.2	18.7	14.9	9.6
E 3.....	76.7	53.5	27.6	32.9	22.6	24.6	21.2
E 2.....	»	»	0.5	0.9	2.0	2.5	0.8
E 1.....	»	»	»	0.9	»	»	«
Ch.....	»	»	7.2	10.4	7.9	15.9	20.0
H.....	10.0	11.2	59.3	54.6	57.1	63.3	60.8
G.....	23.3	12.7	13.6	12.9	14.3	12.1	9.2
HH.....	»	»	»	»	»	»	»
Th.....	66.7	76.1	19.9	22.1	20.7	8.7	10.0

I have seen both these formations, the Subularia and the Ran. reptans formation, in the south country, and I can confirm Helgi Jónsson's statement that they occur on a water-covered soil. The

Subularia formation has been described above, the Ran. reptans formation under the flói (p. 70). There seems, however, to be no little difference between the environment of these two formations. The Subularia formation is found where the motion of the water (temporarily or continually?) is so strong that it causes a shifting of the bottom material, in the Ran. reptans formation it is less strong and no shifting takes place. As the third link in the chain we have the flói; here the water is stagnant and the bottom covered with mosses.

All three formations have but a small density of species and practically the same species group spectrum, a high E percentage and concentration in the central part of the spectrum. The biological spectrum is of special interest. In the Subularia formation Th are dominant, in the R. reptans formation H, and in the flói G.

The Koenigia flag and the flag mo represent the flag vegetation proper. The circling results are tabulated in table 17 A, 3—7.

Nos. 3—5 show the composition of the vegetation on flag at Björk in the south country. The dominant species are in the first place *Koenigia islandica* and *Sedum villosum*. Further *Agrostis alba* and *Juncus* spp. abound, *J. bufonius*; *J. triglumis*, *J. biglumis*, *Triglochin palustre*, *Polygonum viviparum*, *Equisetum arvense*, *Sagina nodosa*, *Minuartia verna*, *Cerastium alpinum*, *C. cæspitosum*, *Deschampsia alpina*, *Festuca ovina*, and *Luzula spicata*. The table gives more precise information as to the part played by the individual species and the variation from locality to locality. Sporadically a number of plants occur which mostly originate from the surrounding formations, jaðar and mo.

Nos. 6—7 represent the flag mo at Lækjamót in the north country. The dominant species are practically the same here (though *Juncus bufonius* was absent in the north country), and the individual species occur with almost the same F.-percentage. An essential difference between the flag mo and the Koenigia flag is due to the presence of a quantity of mo plants in the flag mo, thus especially *Thalictrum alpinum*, *Rumex acetosa*, *Poa alpina* and *P. glauca*, *Parnassia palustris*, *Armeria vulgaris*, *Carex capillaris*, *Silene acaulis* and several others. Another marked difference between the flag mo and the Koenigia flag is the great number of little knolls found in the former.

The individual species are differently distributed over the surface, some species being associated with the clayey soil others with the knolls. On the clayey soil the vegetation is open, and here we

principally or exclusively find such species as *Koenigia islandica*, *Sedum villosum*, *Juncus bufonius*, *biglumis* and *triglumis*, *Triglochin palustre*, *Equisetum arvense*, *Cerastium cæspitosum*, *Sagina nodosa*, *Minuartia verna*. On the small knolls the vegetation is connected and here we find the species *Agrostis alba*, *Deschampsia alpina*, the *Festuca* spp., *Armeria vulgaris*, *Rumex acetosa* and several others, principally such as are common to mo and jathar.

Helgi Jónsson was the first to describe the flag vegetation, though without thus naming it. His description of the vegetation on the "clayey flats" which is referred to the "open vegetation of the lowlands" corresponds to the description given above of the flag vegetation. In "Studier over Øst Islands Vegetation" 1895, p. 86, he says, "they (i. e. the clayey flats) have most frequently a monotonous vegetation consisting of *Sedum villosum*, *Koenigia islandica*, *Juncus triglumis* and other more casually growing plants. This vegetation on clay varies not a little in composition; of the forms I have seen, I note especially the following: a. The vegetation consists only of *Sedum villosum* which occurs in a rather dense growth and gives a fresh appearance to the clayey flats by its pretty flowers. b. The vegetation consists only of *Koenigia islandica* which also occurs in a rather dense growth but in this locality it is most frequently of a red colour. c. The vegetation consists of *Sedum villosum* and *Koenigia islandica* either in equal quantities or with now one, now the other as the dominant. d. The vegetation consists of *Juncus triglumis* as the dominant plant, besides scattered individuals of *Sedum villosum* and *Koenigia islandica*, and *Agrostis alba* in scattered tufts."

"It should be noted that in many places a transition to the mo vegetation is seen where most of the species of the mo occur (*Gramineae*, *Juncaceae*) growing in scattered tufts with bare clay between, it is merely a younger stage of the grass mo."

In "Vegetationen paa Snæfellsnæs" 1900, pp. 43—44, we read: "Plants characteristic of the clayey flats are *Sedum villosum*, *Koenigia islandica*, *Juncus alpinus* and *J. triglumis*. The two first-mentioned are most prominent and often occur in an astonishing quantity. The most frequently occurring species are *Agrostis alba*, *Aira alpina*, *Sagina nodosa*, *Triglochin palustre*, *Epilobium palustre*, *Luzula spicata*, *L. multiflora*. In East Iceland this vegetation had quite the same appearance. When these flats dry up in the summer, they are often divided by cracks into many small polygonal areas,

lozenges, the surface contracting so much owing to the disappearance of the water that it cracks. On the flats here described these are of very different duration, most frequently they last a very short time, disappearing when the surface becomes damp again. For the vegetation these cracks, as far as I can see, are of no importance, since it nearly always occurs on the lozenges themselves."

In "Vegetationen paa Syd Island", 1905, pp. 13—14, he writes, "Open clayey flats are met with in many places." "The vegetation on the clayey flats is always very poor in species, and only where the vegetation of the clayey flats is passing into the surrounding associations do we meet with a greater abundance of species. The typical clayey flats as a rule contain the same species everywhere. The few species which are exclusively or principally found on the clayey flats and must thus be designated as characteristic of them are the following: *Sedum villosum*, *Koenigia islandica*, *Spergula arvensis*, *Juncus alpinus*, *J. triglumis*. The most commonly occurring are *Agrostis alba*, *Juncus bufonius*, *Equisetum arvense*, *Epilobium palustre*, *Poa annua*, *Stellaria crassifolia*, *St. media*, *Cerastium vulgare*, *Polygonum aviculare*, *Sagina procumbens*. More rarely we meet with *Triglochin palustre*, *Alopecurus fulvus*, *Scirpus pauciflorus*, *Eriophorum Scheuchzeri*, *Sedum annum*, *Poa glauca*, *Rumex acetosa*, *Silene maritima*, *Phleum alpinum*, *Myosotis arvensis*, *Veronica serpyllifolia*, *Rumex acetosella*, *Thymus serpyllum*, *Leontodon*."

By the above quotations from H. Jónsson's descriptions of the vegetation and by the circling results given here the flag vegetation has been characterised floristically. If we are to characterise the vegetation biologically, the best way will be to compare the biological spectra of the flag and the neighbouring vegetations, i. e. the mo and the jaðar. Table 18 gives the biological spectra of these types of vegetation at Björk and Lækjamót, viz. respectively moist mo, flag (or flag mo), jaðar (or myri).

It will appear from the table that the flag vegetation is poorer in species and shows less density of species than the surrounding types of vegetation, the mo and the jaðar. This applies especially to the Koenigia flag. As regards the content of Raunkiær's life forms, the flag is especially remarkable by its high Th percentage. As shown above, the Subularia flag had a Th percentage of 71, the Koenigia flag a Th percentage of 20.9, and the flag mo a Th percentage of 9.4. The table likewise shows a comparatively high H percentage and comparatively low Ch and G percentages. The pro-

TABLE 18. Biological Conditions in Mo, Flag, and Jaðar
at Björk (I) and Lækjamot (II). Cf. the text.

a	Number of species	Density of species	Ch	H	G	Th			
I. Moist mo	39.7	14.8	28.9	52.3	18.3	0.1			
Flag	20.0	8.8	8.5	57.0	13.6	20.9			
Jaðar	42.0	13.8	22.3	53.6	24.1	0.2			
II. Moist mo	42.5	15.9	24.7	58.0	14.1	3.3			
Flag mo	29.0	11.0	18.0	62.1	10.7	9.4			
Mýri vegetation	33.0	11.2	12.5	39.9	45.9	2.1			
b	A	E	A 3	A 2	A 1	E 4	E 3	E 2	E 1
I. Moist mo	39.3	60.7	19.3	9.6	10.4	32.6	10.8	16.8	0.5
Flag	52.8	47.2	36.1	16.5	0.1	18.1	27.7	1.1	0.3
Jaðar	35.6	64.4	15.0	8.2	12.5	35.8	13.5	14.9	0.3
II. Moist mo	56.5	43.5	32.6	15.9	8.0	22.6	10.2	8.8	2.0
Flag mo	63.3	36.7	41.5	21.8	»	12.3	22.9	1.7	»
Mýri vegetation	50.0	50.0	22.6	25.1	2.3	24.6	16.5	8.7	»

portion of Th, G, and H is no doubt directly dependent on the comparatively strong desiccation of the flag in the summer.

On passing from the mo to the mýri on gently sloping ground, in places where no flag vegetation has been developed, there will, as will be shown in more detail later on, occur a decrease of the Ch percentage and an increase of the H, Th, and G percentages at the level answering to the flag zone. Apart from the geophytes this is the same change as characterised the flag vegetation. Hence the flag vegetation must not be regarded as such an isolated phenomenon as its physiognomy and peculiar biology would seem to suggest at a first glance, it must be regarded as an extreme stage of development of those conditions of environment which are found and act in the stage of moisture with which the flag vegetation is associated.

If we consider the species group spectrum, here, too, we shall find a peculiar difference between the flag vegetation and the surrounding types. The proportion of arctic plants is comparatively high in the flag, and this is due to a rise in the A 3 and A 2 per-

centages, while the A 1 species are practically absent. In the E sub-groups the peculiarity appears in the fact that the decrease comes especially under E 2 and likewise in no small degree under the E 4 species, while the E 3 percentage is considerably higher than in the surrounding types of vegetation, mo and jaðar or myri. Both the localities examined, the south country as well as the north country, show the same deviation from the adjacent types of vegetation with regard to the species group spectra. The flag vegetation is thus characterised by comparatively high A 3, A 2, and E 3 percentages, and by comparatively low A 1, E 4, and E 2 percentages.

As regards the distribution of the flag vegetation it may be said that in Iceland it seems to be peculiar to the lowlands alone. Personally I have sought the flag vegetation in vain in the highland tracts of South Iceland (Lýngdalsheiði), of Arnarvatnsheiði and Holtavörðuheiði (Tvidägra). Magister Pálmi Hannesson, who has explored the highlands for a number of years, has informed me orally that a flag vegetation has never been observed here. Helgi Jónsson refers the clayey flats (i. e. the flag vegetation) to the "open vegetation of the lowlands" (it is not mentioned that they only occur in the lowlands). If we may infer from this that the clayey flats have not been seen by Helgi Jónsson in the highlands, all observations would seem to indicate that the flag vegetation is limited to the lowlands.

In Iceland the flag vegetation has been observed in all parts of the country. As mentioned above, H. Jónsson has described it from East Iceland, South Iceland, and South-West Iceland. On my journey in the summer of 1925 I observed flag vegetation in the south country (at the foot of Lýngdalsheiði) in the south-west country (Norðtunga in Borgarfjörður), and in the north country (Lækjamót in Viðidalur). According to the oral communication of Mr. Jacob Lindal, the farmer at Lækjamót, who has travelled through the north country as consulting agriculturalist for a number of years, the flag vegetation is of common occurrence throughout this part.

Judging from the literature, the flag vegetation seems to be peculiar to Iceland. I have not been able to find in the phytogeographical literature on the surrounding countries any record of types of vegetation which may be compared with or referred to the flag vegetation in its typical form.

Hence the flag vegetation seems to be a type of vegetation peculiar to the Icelandic lowlands.

The special association of the flag vegetation with the Icelandic lowlands is, however, probably more apparent than real, for the flag vegetation seems to be a northerly, highly specific offshoot of a series of peculiar Th formations which are met with in Denmark, too, on moderately moist soil. These Th formations have not, however, been more closely investigated though they had early attracted the attention of botanists by their peculiar flora. The following are some of the most characteristic species: *Radiola milligrana*, *Linum catharticum*, *Scirpus setaceus*, *Centunculus minimus*, *Myosurus minimus*, *Gnaphalium uliginosum*, a number of small *Juncus* spp. *J. bufonius*, *J. tenuis*, *J. capitatus*, and *J. pygmaeus*, besides *Bulliarda aquatica*. On slightly damper soil we meet with species such as *Subularia aquatica*, *Pilularia globulifera*, *Elatine hexandra*, *Montia* spp., *Ranunculus reptans*, *Juncus supinus*, *Peplis portula*, *Limosella aquatica*. This flora is especially met with on dunes, on damp moors, or in badly cultivated rye fields, and occurs frequently at any rate in western Jutland. In meadows, especially littoral meadows, in addition to a number of species already mentioned, we meet with a number of *Gentiana* spp., *Rhinanthus*, *Euphrasia*, *Odontites*, and *Sagina* species. Even in damp birch woods Th formations may be met with consisting of *Geranium Robertianum* and *Impatiens noli tangere*.

However, it is not only the characteristic life form that is common to the Danish Th formations on soil of moderate moisture and the Icelandic flag, they have also a number of species in common; thus the following species recorded from the flag are found in Denmark in company with the above-mentioned species. *Ranunculus reptans*, *Subularia aquatica*, *Juncus bufonius*, *J. supinus*, *Triglochin palustre*, *Agrostis alba*, *Equisetum arvense*, *Sagina nodosa*, *Parnassia palustris*, *Linum catharticum*, *Rhinanthus minor*, *Spergula arvensis*, *Stellaria media*, *Scirpus pauciflorus*.

A comparison of these lists may perhaps be of aid in tracing the forces which give rise to the flag in Iceland. The causes for the occurrence of the Th formations on moderately moist soil in Denmark must be sought partly in fluctuations in the level of the water, partly in the frost phenomena present here and resulting in crumbling and aeration of the soil. When the moderately moist Th formations attain their finest development in the Icelandic lowlands which are sub-arctic and Atlantic in character, this must no doubt be due to a corresponding increase in these factors, especially the frost phenomena.

C. LÆKJAMÓT (THE NORTH COUNTRY).

With the farm Lækjamót as my starting point I had an opportunity of studying the vegetation in a valley in North Iceland for some days in the middle of August 1925. The principal types of vegetation are the same here as in the south country, viz. melar, mo, and myri. The following applies to their distribution. Up the sides of the valley, at the top only the melar vegetation is met with, lower down there occurs a belt in which the mo prevails with spots of melar, but devoid of myri, and at the foot there is a belt where the myri vegetation is dominant and where mo and melar are only found over small areas. In the bottom of the valley the depressions are occupied by the myri vegetation, the more elevated areas by melar and mo. Along the banks of the rivers the vegetation consists mainly of jaðar. Between the vegetation of the valley sides and that of the valley bottom there is the essential difference that the myri vegetation of the valley sides consists exclusively of halla myri (well myri), while in the valley bottom it consist exclusively of fórmýri (swampy myri). On the boundary line between mo and myri, flag mo was met with, both on the valley floor and on the sides of the valley.

Such is the appearance of a transverse section of a vally in North Iceland. Unfortunately time did not permit me to investigate a longitudinal section. What I have seen fragmentarily would seem to show that at any rate the floor of the valley exhibits typical and interesting differences, especially as regards the myri vegetation. At the head of the valley, where there was no level bottom, the halla myri (including the dý vegetation) extended right down to the river. This was the case at Aðalbol in the Austerádalur. Further out, as at Lækjamót in the Viðidalur, halla myri is only found on the mountain slopes, while the level bottom of the valley is covered with the fórmýri (including the flói vegetation). Still further out the fórmýri seems to have been replaced by the sétmýri, the *Carex cryptocarpa* myri (including the fen vegetation, the *Equisetum limosum* swamp). This at any rate was the case at the mouth of the Vatnsdalur.

Tables 19 A and 20 A show the circling results for melar, mo, and myri in the neighbourhood of Lækjamót. The circling results for the flag mo are given in table 17 A together with the flag vegetation from the south country.

TABLE 19 A. The Mellar and Mo Vegetation at Lækjamót.

1—3 the mellar vegetation, 4—7 the mo vegetation, 4—5 the comparatively dry mo, 6—7 the comparatively moist mo. Localities 1, 5, and 7 are situated at the bottom of the valley N.W. of Lækjamót c. 50 m above sea level; 2, 3, 4, and 6 on the valley slope on the western side of Víðidalssfjall, directly east of Lækjamót c. 75 m above sea level. 4 and 6 were examined on ¹⁹/s 1925, 1, 2, 3, 5, and 7 on ²⁰/s 1925. (1. 20. ¹/₁₀ m², 2—7. 25. ¹/₁₀ m²).

			1	2	3	4	5	6	7
Arabis petræa.....	A 1	Ch	5	12	8	>	>	3	>
Arenaria ciliata	A 3	Ch	10	16	8	>	>	3	3
Minuartia verna.....	A 3	Ch	25	32	12	>	>	3	3
Saxifraga oppositifolia ..	A 3	Ch	10	36	60	>	>	3	3
Dryas octopetala	A 3	Ch	5	44	40	96	72	60	>
Thymus serpyllum	E 4	Ch	50	56	56	84	92	68	52
Armeria vulgaris	A 3	Ch	10	16	16	44	24	28	8
Silene acaulis	A 3	Ch	50	52	60	72	52	40	28
Cerastium alpinum	A 3	Ch	50	56	44	40	16	56	16
Luzula spicata	A 2	H	45	48	48	64	60	44	48
Poa glauca.....	A 3	H	25	60	44	24	24	24	16
Festuca ovina	E 4	H	50	44	44	28	32	48	68
— rubra	E 4	H	5	40	52	96	88	84	96
Agrostis canina	E 3	H	5	12	8	68	92	80	92
Galium Normannii.....	A 1	H	10	20	48	32	60	72	64
Euphrasia latifolia	A 2	Th	10	20	20	44	16	28	24
Salix herbacea	A 3	Ch	>	4	20	52	80	56	60
Selaginella selaginoides ..	A 1	Ch	>	12	16	60	52	48	36
Juncus trifidus.....	A 2	H	>	8	20	44	60	60	40
Elyna Bellardi	A 3	H	>	24	12	80	92	68	88
Carex capillaris	A 3	H	>	44	28	68	92	76	40
Polygonum viviparum ..	A 3	G	>	52	48	100	96	100	80
Thalictrum alpinum.....	A 2	H	>	32	40	96	92	100	64
Trisetum spicatum	A 3	H	>	12	24	>	40	4	24
Tofieldia palustris.....	A 2	H	>	4	24	52	36	8	8
Empetrum nigrum	E 4	Ch	>	4	>	88	96	72	52
Vaccinium uliginosum...	E 4	Ch	>	>	>	56	80	68	28
Equisetum arvense	E 4	G	>	4	4	20	40	28	20
— pratense	E 2	G	>	8	>	24	52	24	32
Carex rigida	A 3	G	>	>	4	60	48	80	44
Luzula multiflora	E 3	H	>	>	>	28	12	32	24
Poa alpina	A 2	H	>	>	>	16	4	40	12
Pingvicia vulgaris	E 4	H	>	>	4	12	40	8	12
Rumex acetosa	E 3	H	>	>	>	8	8	40	4
Deschampsia caespitosa..	E 2	H	5	>	>	4	>	52	36
Carex sparsiflora	A 1	G	>	>	>	>	12	4	16
Agrostis alba	E 3	H	>	>	>	4	>	>	>
— tenuis	E 2	H	>	>	>	>	>	>	8

TABLE 19 A CONTINUED.

		1	2	3	4	5	6	7
Anthoxanthum odoratum.							8	
Bartschia alpina	E 3	H					4	
Betula nana	A 2	H			16			
Botrychium Lunaria.....	A 2	Ch			4	8	8	
Carex alpina.....	E 4	G						8
Cerastium caespitosum ..	A 2	H						4
Deschampsia flexuosa....	E 3	Ch			8			
Draba incana	E 3	H					4	12
Equisetum variegatum...	A 2	H	5				40	
Galium verum	A 3	H		4	4			36
— boreale	E 1	H						
Gentiana aurea	E 2	H				4		56
— campestris	A 1	Th						
— tenella.....	E 1	H			4			20
Habenaria viridis	A 2	Th					12	
Koenigia islandica.....	A 1	G						
Parnassia palustris	A 3	Th			24			
Plantago maritima	E 2	H			8			
Rhinanthus minor	E 4	H				52		
Rumex acetosella.....	E 2	Th				4		
Sagina nodosa	E 4	H	65					
Salix glauca	E 3	H				16		
Sedum villosum.....	A 3	Ch				12		
Silene maritima.....	A 2	H				4		
Viola canina.....	A 1	Ch	10					
— palustris	E 3	H					12	
	E 3	H						8

The Melar Vegetation. Cf. Table 19 A, 1—3.

Locality No. 1 represents the vegetation in an area of the bottom of the valley at Lækjamót, swept bare by the wind; Nos. 2 and 3, on the other hand, are from the foot of Viðdalsfjall. In all three localities the vegetation was open, not covering the substratum entirely; in No. 1 the surface was covered with gravel and stones without any appreciable trace of solifluction, in Nos. 2 and 3, on the other hand, there was polygonal formation and solifluction.

Compared with the mo vegetation, the Ch, A, and especially the A 3 species play a comparatively prominent part, whereas G and the lower E sub-groups are very sparsely represented. The most conspicuous species are *Cerastium alpinum*, *Silene acaulis*, *Armeria vulgaris*, *Thymus serpyllum*, *Dryas octopetala*, *Luzula spicata*, *Festuca ovina* and *rubra*, *Poa glauca*, *Agrostis canina*, *Euphrasia latifolia*,

TABLE 19 B.

Biological Spectra of the Melar- and Mo Vegetation at Lækjamót.

	1	2	3	4	5	6	7
Points sum	450	780	828	1776	1704	1748	1420
Number of species	20	30	31	42	36	41	44
Density of species	4.5	7.8	8.3	17.8	17.0	17.5	14.2
A	60.0	77.9	79.2	66.0	62.0	60.0	52.1
E	40.0	22.1	20.8	34.0	38.0	39.1	47.9
A 3.....	41.1	57.9	52.2	40.3	38.3	36.2	29.0
A 2.....	13.3	14.4	18.4	18.9	16.4	16.9	14.9
A 1.....	5.6	5.6	8.7	6.8	7.3	7.8	8.2
E 4.....	38.9	19.0	19.3	21.8	27.5	21.5	23.7
E 3.....	1.1	1.5	1.0	6.8	7.3	9.4	11.0
E 2.....	»	1.0	0.5	5.4	3.1	8.2	9.3
E 1.....	»	0.5	»	»	0.2	»	3.9
Ch	50.0	43.6	41.1	35.1	34.5	29.1	20.3
H	47.8	45.6	48.8	48.4	50.0	52.2	63.7
G	»	8.2	6.8	12.8	14.6	14.2	14.1
HH	»	»	»	»	»	»	»
Th	2.2	2.6	3.4	3.6	0.9	4.6	2.0

Galium Normanni, *Saxifraga oppositifolia*, *Arenaria ciliata*, *Minuartia verna*, and *Arabis petræa*. The last four species are only found in melar, the others also in the mo where, however, their physiognomic effect is obscured by more dominant plants.

Of species peculiar to the melar vegetation at Lækjamót we may especially mention *Rumex acetosella* and *Silene maritima*, while the following species are characteristic of the melar at Viðidalsfjall: *Salix herbacea*, *Selaginella selaginoides*, *Juncus trifidus*, *Elyna Bellardi*, *Carex capillaris*, *Trisetum spicatum*, *Polygonum viviparum*, *Tofieldia palustris*, and *Thalictrum alpinum*. None of these species are specific to melar, they may all be found in the surrounding mo formations.

The Mo Vegetation. Table 19 A, 4—7.

On the mo vegetation I was able to analyse 4 localities, 2 at high and 2 at low levels, one set at the bottom of the valley and one on the slope.

The surface of the mo is knolly here as elsewhere, but the top

of the knolls, especially on the side facing the sea (north), had sometimes been deprived of its carpet of vegetation, exposing the loose interior of the knoll to the desiccating and eroding action of the wind. Hence large areas of the valley bottom have been transformed into barren stretches of gravel covered with the molar vegetation described above.

The number and density of species — especially the latter — are comparatively high in the mo both in comparison with the surrounding vegetations and with the mo vegetation in other parts of Iceland. The greatest density hitherto demonstrated, viz. 17.8, was found on the mountain slopes of Viðidalsháll. H play a very prominent part in the composition of the vegetation, while Ch have decreased. The G percentage has increased while the Th percentage is unaltered, c. 3. The species group spectrum shows a change in the same direction. The A and especially the A 3 species have decreased in quantity, whereas the E species, especially the lower sub-groups, have increased.

Even if the chamaephytes are of subordinate importance in respect of species and points, species such as *Dryas octopetala*, *Empetrum nigrum*, *Vaccinium uliginosum*, and *Thymus serpyllum* are physiognomic. Of other dominant chamaephytes we may mention *Cerastium alpinum*, *Silene acaulis*, *Armeria vulgaris*, and *Salix herbacea*. Grasses and cyperaceous plants play a very prominent part, especially *Elyna Bellardi*; further *Luzula spicata*, *L. multiflora*, *Juncus trifidus*, *Carex capillaris*, *C. rigida*, and *C. sparsiflora*, *Festuca ovina* and *F. rubra*, *Poa glauca* and *P. alpina*, *Agrostis canina*, and *Trisetum spicatum*. Of herbaceous plants we find especially *Polygonum viviparum*, and *Thalictrum alpinum*, further *Rumex acetosa*, *Tofieldia palustris*, *Pinguicula vulgaris*, and *Galium Normanni*; of pteridophytes *Selaginella selaginoides* and *Equisetum* spp., thus *Equisetum arvense*, *E. pratense*, and *E. variegatum*. The Th are *Euphrasia latifolia*, *Rhinanthus minor*, and *Gentiana* spp.

Some floristic differences may be shown to exist between the different types of mo. In the low mo *Deschampsia caespitosa* will always be met with; even though the F.-percentage is not very high, the species is physiognomically fairly predominant. *Carex sparsiflora* is also more frequently met with in the low mo than at higher levels.

In the mo of the valley slopes the following species not found at the bottom are met with. *Equisetum variegatum*, *Rhinanthus minor*, *Habenaria viridis*, *Parnassia palustris*, and *Bartschia alpina*.

It is chiefly these species which cause the greater density of species on the valley slopes.

Biological differences also occur. Thus the Ch percentage is higher in the high than in the low mo, whereas the reverse is the case with the H percentage. The high E percentage of locality No. 7 is due to a deeper and more constant snow-covering in the winter.

The Mýri Vegetation. Cf. table 20 A, 1—7.

Owing to the short time at disposal only a very few of the mýri formations were investigated; these were a series of moist formations in the halla mýri (1—5), and a couple of formations in the fórmýri (6—7).

The halla mýri is only found along the foot of mountains, and it is essential to its occurrence that the ground-water comes to the surface. This causes a peculiar difference between the halla mýri (well mýri) and the fórmýri (swampy mýri). In the fórmýri the amount of moisture is determined by the precipitation on and around the depressions in the mýri; the quantity of nutrition supplied by the precipitation is comparatively small or nil, just as also the temperature conditions are relatively closely dependent on the temperature of the air. In the halla mýri the nutrient salts are constantly renewed by the ground water, the temperature of which will more or less influence the temperature of the soil according to its amount. The temperature of the ground water is constant throughout the year, that is to say, it is equal to the mean annual temperature in the locality in question. Thus the halla mýri will be warmer in the winter but cooler in the summer than the swampy mýri. As a result the species group spectra differ widely. The lower E sub-groups (E 3 and E 2) dominate in the halla mýri owing to the favourable temperature conditions in the winter (!) and A 2 and A 3 species owing to the cool summer soil (!), while the A 1 species are peculiar to the flói of the fórmýri.

Owing to the larger amount of nutrition the number and density of the species is greater in the halla mýri than in the fórmýri, especially in the dampest areas. The biological spectra agree in regard to the preponderance of the geophytes, while there is an essential difference in the chamaephytes, the Ch percentage being highest in the fórmýri.

In the halla mýri the physiognomical dominant is *Equisetum dalustre*, as in the fórmýri it is *Carex Goodenoughii* besides *Erio-*

TABLE 20 A. The Mýri Vegetation at Lækjamót.

Localities 1—5 situated at the foot of Viðidalsfjall on its western side c. 75 m above sea level and represent Halla mýri of various degrees of moisture. 6—7 situated at the bottom of the valley c. 50 m above sea level, Fór mýri. 1, 3, 6, and 7 examined on ²¹/s 1925; 2, 4, and 5 on ²²/s 1925. (25. $\frac{1}{10}$ m²).

			1	2	3	4	5	6	7
Carex panicea	E 3	G	84	8	8	»	»	16	
Scirpus caespitosus.....	E 4	H	76	4	4	12	»	8	
Carex microglochin.....	A 2	G	80	20	32	36	»	»	
— capillaris	A 3	H	84	96	20	»	»	12	
Tofieldia palustris	A 2	H	56	24	»	»	»	8	
Pingvicia vulgaris	E 4	H	44	32	»	»	»	8	
Equisetum variegatum ..	A 3	H	»	48	12	»	4	»	
— palustre	E 2	G	60	96	64	88	84	»	
Luzula multiflora	E 3	H	16	60	8	»	»	16	
Bartschia alpina	A 2	H	24	48	»	»	»	»	
Calamagrostis neglecta ..	E 4	H	»	16	12	»	52	4	
Trigochin palustre	E 4	H	»	»	20	40	64	»	
Menyanthes trifoliata ..	E 4	HH	»	»	48	48	4	»	
Juncus alpinus	E 3	H	4	»	4	52	36	»	
Eriophorum Scheuchzeri.	A 3	HH	»	»	»	»	56	»	
Carex Lyngbyei	E 3	G	»	»	»	»	100	»	
Eriophorum polystachyum	E 4	G	96	16	24	32	40	96	100
Polygonum viviparum ...	A 3	G	100	100	88	52	»	76	
Thalictrum alpinum	A 2	H	40	84	44	»	»	60	
Carex Goodenoughii	E 3	G	72	92	96	100	56	76	
— rariflora	A 2	G	40	96	100	100	60	68	
— chordorrhiza	A 1	G	12	»	68	20	»	8	100
— dioica	E 4	G	»	»	»	»	»	84	
— saxatilis	A 3	G	16	»	4	»	»	68	4
Vaccinium uliginosum ...	E 4	Ch	92	80	68	4	»	96	
Betula nana	A 2	Ch	»	»	4	»	»	68	
Agrostis alba	E 3	H	»	4	4	»	»	»	
— canina	E 3	H	»	»	4	»	»	»	
Anthoxanthum odoratum.	E 3	H	»	»	»	»	»	8	
Cardamine pratensis....	E 4	H	4	»	»	»	»	12	
Carex rigida	A 3	G	»	16	»	»	»	8	
— rostrata	E 3	HH	»	»	12	»	»	»	
Cerastium caespitosum ..	E 3	Ch	»	32	»	»	»	»	
Deschampsia caespitosa..	E 2	H	»	4	»	»	»	»	
Dryas octopetala	A 3	Ch	»	12	»	»	»	»	
Elyna Bellardi	A 3	H	»	»	»	»	»	4	
Empetrum nigrum	E 4	Ch	4	4	»	»	»	32	

TABLE 20 A. CONTINUED.

		1	2	3	4	5	6	7
Euphrasia latifolia	A 2	Th	4	36	4	4	»	»
Festuca ovina	E 4	H	4	12	4	»	»	24
— rubra	E 4	H	»	48	»	»	4	32
Galium Normannii	A 1	H	»	12	4	»	»	»
Gentiana amarella	E 2	H	8	»	»	»	»	»
Juncus arcticus	A 2	G	»	4	»	»	»	»
— trifidus	A 2	H	»	»	»	»	4	»
— triglumis	A 3	H	4	4	8	12	12	»
Luzula spicata	A 2	H	4	»	»	»	»	»
Parnassia palustris	E 2	H	»	20	»	»	»	»
Poa glauca	A 3	H	»	4	»	»	»	»
Rhinanthus minor	E 2	Th	4	4	»	»	»	»
Salix glauca	A 3	Ch	4	12	»	»	»	»
— herbacea	A 3	Ch	»	4	4	»	8	»
Silene acaulis	A 3	Ch	»	4	»	»	»	»
Thymus serpyllum	E 4	Ch	»	4	»	»	»	»

TABLE 20 B.

Biological Spectra of the Mýri Vegetation at Lækjamót.

	1	2	3	4	5	6	7
Points sum	1048	1180	780	600	572	908	204
Number of species	29	37	29	14	13	27	3
Density of species	10.5	11.8	7.8	6.0	5.7	9.1	2.0
A	45.4	54.6	51.3	37.3	23.1	43.6	51.0
E	54.2	45.4	48.7	62.7	76.9	56.4	49.0
A 3	19.8	25.4	17.4	10.7	12.6	19.4	2.0
A 2	23.7	26.4	23.6	23.3	10.5	22.9	»
A 1	1.9	2.7	10.3	3.3	»	1.3	49.0
E 4	30.5	18.3	23.1	22.6	28.7	43.6	49.0
E 3	16.8	16.6	17.4	25.4	33.6	12.8	»
E 2	6.9	10.5	8.2	14.7	14.7	»	»
E 1	»	»	»	»	»	»	»
Ch	10.3	14.6	10.8	0.7	»	22.9	»
H	35.1	44.6	19.0	19.3	30.1	22.0	»
G	53.8	38.0	62.1	71.3	59.4	55.1	100.0
HH	»	»	7.7	8.0	10.5	»	»
Th	0.8	3.4	0.5	0.7	»	»	»

phorum polystachyum, and in the fótmyri *Carex Lyngbyei*. Of other plants it is mostly Cyperaceæ which are found intermixed with *Equisetum palustre*, thus species like *Eriophorum polystachyum*, *Carex Goodenoughii*, *C. rariflora*, *C. microglochin*, *C. capillaris*, *C. panicea*, and *C. chordorrhiza*, besides *Scirpus cespitosus*. Other more conspicuous plants are *Polygonum viviparum*, *Thalictrum alpinum*, *Luzula multiflora*, *Bartschia alpina*, *Tofieldia palustris*, *Pinguicula vulgaris*, *Selaginella selaginoides*, and *Equisetum variegatum*; of Ch only *Vaccinium uliginosum* occurs with any noticeably high F.-percentage.

Locality No. 2 represents the typical, i. e. the most widespread halla myri formation; No. 1 is from a somewhat high level, Nos. 4—5 from rather damp soil. If the water in the depression is stagnant, *Carex rariflora* will be the physiognomical dominant (cf. No. 4), if it contains running water, *Carex Lyngbyei* will dominate, perhaps in company with *Eriophorum Scheuchzeri* (cf. Nr. 5). The two formations can be recognised, even at a distance, by their colours, the *Carex rariflora* formation by a darkgreen hue, the *Carex Lyngbyei* formation by its yellowish green tinge. The surface differs from the typical formation by being devoid of knolls.

Where springs are formed in the halla myri, a moss vegetation will develop. On this vegetation, the dý, Helgi Jónsson writes as follows (1900, p. 25): — “the moss pools occur most frequently at the foot of the mountains where the numerous springs appear; here they pass imperceptibly into the myri.” “The mosses which seem to predominate are *Philonotis fontana* and *Mniobryum albicans v. glacialis*.” “Scattered here and there in the moss carpet there occur *Epilobium alsinefolium*, *E. Hornemannii*, *Cerastium trigynum*, *Montia rivularis*, *Saxifraga rivularis*, *Ranunculus hyperboreus*, and *Catabrosa aquatica*. In addition there occur *Epilobium palustre*, *E. lactiflorum*, *Eriophorum Scheuchzeri*, *Carex cryptocarpa*, *C. canescens*, *Eriophorum angustifolium*, *Equisetum palustre*, *Carex rariflora*, *Menyanthes* and *Saxifraga stellaris*.

The mosses are exclusively dominant; the intermixed species are both few and far between.”

The fómýri is only found at the bottom of the valley. An essential difference between halla myri and fómýri is this that *Equisetum palustre* is lacking in the fómýri, *Betula nana* in the halla myri. The most conspicuous plants are *Eriophorum polystachyum*, *Vaccinium uliginosum*, and *Betula nana*, further *Carex Goodenoughii*, *rariflora*, *saxatilis*, and *dioica*, besides *Polygonum viviparum* and

Thalictrum alpinum. Of minor importance are *Festuca ovina*, *F. rubra*, *Cardamine pratensis*, and *Empetrum nigrum*.

Where the ground-water covers the soil throughout the year the knolls disappear, the surface is level, and the flói vegetation is formed (cf. table 20,7). The dominant species are *Eriophorum polystachyum* and *Carex chordorrhiza*.

D. NORDTUNGA.

In the preceding part we have dealt with all the lowland types of vegetation except the forest. In the following I shall give a description of it in so far as I was able to examine it during a couple of days' stay on the farm Norðtunga in Borgarfjörður.

Here the forest occurs both at the bottom of the valley and on the sunny northern slope, but not on the shady southern slope. The succeeding investigations, however, apply especially to the forest at the bottom of the valley.

Viewed from one of the valley slopes the forest does not appear as a continuous growth in the sense that the trees are equally distributed over the entire area of growth, but open patches where the birch is low, very scattered, or entirely absent, alternate with stretches where the growth is denser. It was, however, especially on the outskirts that this was the case, in the interior of the forest the growth was continuous.

Fig. 14 shows a glade in the forest. The soil is full of large knolls.

The statistical results are given in table 21 A. Nos. 1—2 are from the forest itself, 3—6 from the glades in the forest, No. 7, finally, is the mo some distance outside the forest between the latter and the farm.

On the forest-ground proper grasses are dominant, the following being the most numerous: *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Agrostis canina* and *A. tenuis*, further *Festuca rubra*; of herbaceous plants there occur *Thalictrum alpinum*, *Carex rigida*, *Galium boreale* and *Normanni*, and *Polygonum viviparum*. The chamaephytes are of minor importance, *Vaccinium uliginosum* and *Empetrum nigrum* are found here and there.

The vegetation of the glades occupies an intermediate position between the forest-ground and the mo. The species known from the forest-ground recur here, moreover a number of typical

TABLE 21 A. The Forest Undergrowth at Nordtunga.

Localities 1—2 represent forest undergrowth below dense birch copses, 3—6 the vegetation in open birch copses or glades; 7 is the mo vegetation outside the forest. 1, 4 and 6 examined on ²⁵/s 1725, 3 on ²⁶/s, 2, 5 and 7 on ²⁷/s 1925. (25. $\frac{1}{10}$ m²).

			1	2	3	4	5	6	7
Betula pubescens	E 3	F	100	100	88	24	4	4	3
Deschampsia flexuosa....	E 3	H	96	100	80	76	80	84	16
Anthoxanthum odoratum	E 3	H	68	48	48	68	64	92	4
Agrostis canina	E 3	H	60	60	44	96	60	88	92
Festuca rubra	E 4	H	52	44	76	76	92	88	96
Thalictrum alpinum....	A 2	H	60	60	60	80	76	96	80
Carex rigida	A 3	G	44	76	60	80	64	76	72
Galium boreale	E 2	H	32	48	80	72	68	92	72
— Normannii	A 1	H	36	4	32	64	60	56	68
Polygonum viviparum ...	A 3	G	36	12	44	64	60	76	76
Vaccinium uliginosum...	E 4	Ch	36	24	88	92	84	76	88
Empetrum nigrum	E 4	Ch	24	8	56	76	72	84	84
Juncus trifidus.....	A 2	H	8	4	20	40	28	20	60
Festuca ovina	E 4	H	4	16	20	52	48	32	64
Galium verum	E 1	H	8	8	44	56	56	36	3
Luzula multiflora	E 3	H	8	8	48	36	24	20	12
Elyna Bellardi	A 3	H	»	»	4	32	16	8	84
Thymus serpyllum	E 4	Ch	»	»	12	4	20	»	88
Salix herbacea	A 3	Ch	»	»	»	12	8	8	64
Equisetum pratense	E 2	G	»	36	4	»	32	»	52
Luzula spicata	A 2	H	»	»	4	4	»	»	48
Selaginella selaginoides ..	A 1	Ch	»	»	4	12	»	4	40
Silene acaulis	A 3	Ch	»	»	»	»	»	»	32
Agrostis tenuis.....	E 2	H	»	36	64	»	12	»	12
Armeria vulgaris	A 3	Ch	»	»	»	»	»	»	4
Botrychium Lunaria	E 4	G	»	»	»	»	»	4	3
Cardamine pratensis....	E 4	H	»	28	»	8	12	8	»
Cerastium alpinum	A 3	Ch	4	»	»	»	»	»	4
— caespitosum	E 3	Ch	4	4	»	»	»	»	»
Equisetum arvense	E 4	G	»	»	»	8	»	4	16
— variegatum...	A 3	H	»	»	4	»	»	»	»
Erigeron neglectus	A 1	H	»	»	»	8	»	»	4
Euphrasia latifolia	A 2	Th	»	»	»	»	»	»	4
Geranium sylvaticum ...	E 3	H	»	»	20	»	»	»	»
Hieracium sylvaticum...	E 2	H	»	»	4	»	»	»	»
Hierochloë odorata	E 2	G	»	»	»	»	»	4	»
Leontodon autumnalis...	E 3	H	»	4	32	4	4	20	»
Pingvicia vulgaris	E 4	H	»	»	4	4	»	»	24

TABLE 21 A. CONTINUED.

			1	2	3	4	5	6	7
Poa alpina.....	A 2	H	4	»	»	»	»	»	»
-- glauca.....	A 3	H	12	8	»	»	»	»	»
-- pratensis	E 4	G	»	12	»	»	»	12	»
Potentilla verna.....	A 2	H	»	»	»	8	4	»	12
Ranunculus acer	E 4	H	»	8	»	»	»	»	»
Rubus saxatilis	E 3	H	»	»	4	»	»	»	»
Rumex acetosa.....	E 3	H	8	8	4	»	»	»	4
Taraxacum officinale	E 2	H	»	4	12	»	8	12	»
Trisetum spicatum	A 3	H	»	»	»	16	4	4	16
Viola palustris	E 3	H	»	4	8	»	8	16	»

TABLE 21 B. Biological Spectra of 21 A.

	1	2	3	4	5	6	7
Points sum.....	704 (604)	772 (672)	1072 (984)	1172 (1148)	1068 (1064)	1124 (1120)	1392
Number of species	20	26	30	27	26	27	31
Density of species.....	6.0	6.7	9.8	11.5	10.6	11.2	13.9
A	29.0	21.2	21.6	35.8	30.0	31.0	48.0
E	71.0	78.8	78.4	64.2	70.0	69.0	52.0
A 3.....	13.6	12.4	10.4	17.4	14.2	15.3	25.3
A 2.....	10.2	8.3	7.8	11.3	10.1	10.3	14.7
A 1.....	5.1	0.5	3.4	7.2	5.6	5.3	8.0
E 4.....	16.5	18.1	23.9	27.3	30.7	27.4	33.0
E 3.....	48.9	43.5	35.1	25.9	22.8	28.8	9.2
E 2.....	4.5	16.1	15.3	6.1	11.2	9.6	9.8
E 1.....	1.1	1.0	4.1	4.8	5.2	3.2	»
Ch*.....	11.3	5.4	16.3	17.1	17.3	15.4	29.0
H.....	75.5	74.4	72.8	69.7	68.0	68.9	55.2
G.....	13.2	20.2	11.0	13.2	14.7	15.7	15.5
HH	»	»	»	»	»	»	»
Th.....	»	»	»	»	»	»	0.3

mo plants begin to appear, though only here and there. Grasses still dominate, thus *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Agrostis canina*, *Festuca rubra* and *ovina*, *Luzula multiflora*, *Juncus*

trifidus, and *Carex rigida*; some herbaceous plants likewise occur, thus *Polygonum viviparum*, *Thalictrum alpinum*, *Galium boreale*, *Normanni*, and *verum*. The chamaephytes *Vaccinium uliginosum* and *Empetrum nigrum* occur with as high an F.-percentage in the mo.

The mo is the typical Icelandic mo, with the same species that occur elsewhere; selected at random the most conspicuous plants are: *Agrostis canina*, *Festuca rubra* and *ovina*, *Carex rigida*, *Polygonum viviparum*, *Thalictrum alpinum*, *Galium boreale* and *Normanni*, *Vaccinium uliginosum*, *Empetrum nigrum*, *Juncus trifidus*, *Luzula spicata*, *Selaginella selaginoides*, *Elyna Bellardi*, *Thymus serpyllum*, *Salix herbacea*, *Trisetum spicatum*, and *Silene acaulis*.

The following essential difference between the mo and the forest-ground vegetation may be noted. The mo vegetation is characterised by Ch and A species, the forest-ground vegetation by H, especially grasses, and E species. These differences will no doubt prove greater upon closer investigation. The forest-ground at Norðtunga was non-typical in so far as a series of typical forest-ground plants such as *Fragaria vesca*, *Rubus saxatilis*, *Geum rivale*, *Brunella vulgaris*, *Trifolium repens*, *Geranium silvaticum*, *Vaccinium myrtillus*, *Arctostaphylos uva ursi*, *Calluna vulgaris* and several others did not occur here.

V. THE ICELANDIC HIGHLAND FORMATIONS.

No thorough investigations of the highland vegetation which might serve as a basis for comparison with the lowland vegetation and the vegetation in other localities in the highlands having so far been carried out, I have endeavoured to furnish such a basis by my investigations. By its geographical position, its height above sea level, and the grandeur of its scenery, Tvíðágra, the highland plateau west of Langjökull, seemed to me best fitted for such a purpose. Hence the investigations described below have been carried out there, that is, more precisely indicated, in the region round Úlfsvatn on Arnarvatnsheiði.

Before I proceed to a more detailed description of my own investigations I shall give an account of what is known about the highland vegetation. The first more comprehensive description is that of St. Stefánsson (1894). On p. 199 Stefánsson writes: "At the Vatnsdalshals and on the high plateau we especially meet with three formations, viz. the myri, mellar and heather mo vegetations." The latter I found best developed in the so-called "Helgavatnsnupar", gravelly heights on the eastern margin of the Vatnsdalshals. The depressions between these are more or less, and sometimes entirely, covered with a greenish-brown carpet formed of *Empetrum nigrum*, *Vaccinium uliginosum*, and *Betula nana* completely mixed up with each other. *Salix herbacea* and *glauca* also occur almost everywhere throughout this carpet, whereas *Salix lanata* appears only here and there. *Loiseleuria procumbens* is found in no small quantity in several places, and *Cassiope hypnoides* is met with here and there. In several places the dwarf birch predominates over the crowberry (*Empetrum nigrum*), but as a rule the latter is dominant. Of other plants I shall mention first *Dryas octopetala*, which is hardly ever absent from any Icelandic heather mo, next *Thymus serpyllum*, *Polygonum viviparum*, *Galium silvestre*, *Silene*

acaulis, *Armeria* (here and there), *Cerastium alpinum*, *Tosfieldia borealis*, *Juncus trifidus*, *Luzula spicata* and *L. multiflora*, *Alchemilla alpina*, *Pingvicia vulgaris*, *Carex rigida*, *Festuca rubra*, and further, where the soil is a little damp, *Saxifraga Hirculus*, and *Sedum villosum*".

On the high plateau to the south of Vatnsdalur the heather mo is "stunted and patchy" and "the gravelly subsoil comes to the surface everywhere." The composition of the species is as follows: *Empetrum*, *Betula nana*, *Salix glauca*, (here and there), *Salix herbacea*, a very scattered growth of *Vaccinium uliginosum*, *Dryas octopetala*, (rather sparingly), *Elyna Bellardi*, *Silene acaulis*, *Armeria maritima*, *Cerastium alpinum*, *Polygonum viviparum*, *Trisetum spicatum*, *Poa caesia*, *Festuca ovina v. vivipara*, *Thalictrum alpinum*, and *Arabis petreæ*.

The melar vegetation on Vatnsdalshals is described as follows; "Silene acaulis and in some places Dryas are the most conspicuous plants, notably in the flowering season but, in addition to these and several other plants growing among the heather, there also occur Silene maritima, *Saxifraga oppositifolia*, *S. decipiens*, *S. nivalis*, and on high, almost quite bare, gravelly flats *Arenaria ciliata*, *Alsine verna*, *f. propinqua*, *Arabis petræa f. glabra* and *hispida*, *Draba verna*, *Trisetum subspicatum*, *Rumex acetosella*, *Armeria maritima* and others."

In the highlands south of the valley the melar vegetation "resembles that of Vatnsdalshals, but is much poorer in species."

On Vatnsdalsfjall, "on the gravelly crest of the mountain, c. 2000' above the sea, the typical mountain field or melar vegetation, where the plants occur in isolated specimens with large bare patches between, attains its full development, almost without the invasion of any foreign elements. I observed the following species: *Ranunculus glacialis*, *Luzula arcuata*, (both characteristic of high mountains), *Luzula spicata*, *Poa pratensis*, *P. alpina* (*vivipar*), *P. caesia*, *Aira alpina*, *Saxifraga nivalis*, *S. oppositifolia*, *S. hypnoides*, *Cerastium alpinum*, *Erigeron alpinus*, *Polygonum viviparum*, *Silene acaulis*, *Dryas octopetala* (in small quantity), *Potentilla maculata*, *Ranunculus acer*, *Armeria sibirica*, *Salix herbacea*, *Trisetum subspicatum*."

On Víðidalsfjall, at a height of c. 3000' the melar vegetation had the following composition: *Silene acaulis*, *Saxifraga oppositifolia*, *Sedum acre*, *Ranunculus glacialis*, further *Cerastium alpinum f. lanata*, *Poa alpina*, *Aira alpina*, *Poa caesia*, *Saxifraga hypnoides*, *S. decipiens*,

Polygonum viviparum, *Silene acaulis*, *Armeria maritima*, *Salix herbacea*, *Arabis petræa*, *A. alpina*, *Saxifraga cernua* and *S. nivalis*.

The third type of vegetation mentioned by Stefánsson is the móri vegetation. This is described as follows in pp. 201—203. “On Grimstungnaheiði to the south-west of Vatnsdalur I met with a rather widespread form of vegetation which somewhat resembled the usual heather mo by its uneven, more or less knolly surface and its greyish hue, but the soil is rather damp, at least in the early summer, and here *Grimmia hypnoides* is entirely dominant, covering large areas completely.” These moss moes “which must in the main be regarded as transitional between the heather mo and the extensive vegetation of the pools” are poor in flowering plants, though *Cassiope hypnoides* and *Pedicularis flammea* are of common occurrence.

On the vegetation proper of the pools Stefánsson writes: “even at a distance two variations of this vegetation may easily be distinguished, the brownish *Eriophorum* pools characterised by *Eriophorum angustifolium* and the bluish-green *Carex* pools, where the bluish or greyish-green *C. ampullacea* is the dominant plant. This difference is so striking that the peasants have a special term for each of these; the former, the *Eriophorum* pools, are called “Brokflá”, while the latter pools are called “Ljosastrar flá”. They also differ somewhat with regard to composition of species. In the *Eriophorum* pools *Carex pulla*, *C. alpina*, *C. vulgaris*, and *C. hyperborea* are the most conspicuous, whereas, in the *Carex* pools, *Carex rariflora*, *C. vaginata*, and *C. vulgaris* are very common, likewise *Juncus biglumis*. But as a whole this vegetation of the highland pools is extremely poor in species, and of dicotyledons I only observed very few” e. g. *Cardamine pratensis* and *Stellaria crassifolia*.

“Below, on Vatnsdalshals the vegetation of the pools is somewhat richer and more like that of the pools at the bottom of the valley, though not nearly so luxuriant. It consists in the main of the common sedges, e. g. *Carex vulgaris*, *C. chordorrhiza*, *C. rariflora* and *C. rigida*, *Eriophorum polystachyum*, and *Scirpus cæspitosus*.”

These are the three types of vegetation, mo, mellar, and móri, occurring in the highland tracts around Vatnsdalur. However, from the descriptions we must assume that, in addition to these three, there occurs a fourth type viz. the geiri or snow patch vegetation. Thus Stefánsson, when dealing with the vegetation on Viðidalshals, on p. 196, writes as follows: “Some of the little grooves

extending like green or brownish-green bands down the greyish slopes were, where the soil was damp, overgrown with grass and cyperaceous plants, others, on the other hand, had a dwarfish heath vegetation where as usual *Empetrum* was dominant in company with *Vaccinium uliginosum* and *Salix herbacea*. In the greater depressions this heath vegetation was very abundant. In such a depression I observed: *Empetrum*, *Vaccinium uliginosum* and *Myrtillus*, *Salix herbacea* and *glaucia*, *Anthoxanthum odoratum*, *Leontodon autumnalis*, *Phleum alpinum*, *Rumex acetosa*, *Coeloglossum viride*, *Aira flexuosa* and several others."

"On small flat, sometimes almost horizontal, ledges far up the mountain, c. 1500—2000' above the sea, but notably in the cup-shaped depressions and smaller round valleys where the snow remains until far into the early summer, and a layer of humus has gradually formed on the rocky bottom, the dwarf willow becomes entirely dominant. This small very hardy dwarfish growth in such localities forms a dense "half-inch wood" which covers large areas of the barren rocky ground like oases." Of flowering plants I noted the following in a large area of dwarf willows: *Salix glauca* (few and small specimens), *Poa alpina*, *Aira alpina*, *Thalictrum alpinum*, *Cerastium alpinum*, *Thymus serpyllum*, *Erigeron alpinus*, *Luzula spicata*, *L. arcuata*, *Galium silvestre*, *Oxyria digyna*, *Armeria maritima*, *Phleum alpinum*, *Polygonum viviparum*, *Festuca rubra*, *Ranunculus acer*, *Gnaphalium supinum*, *Rumex acetosa*, *Carex lagopina*, *C. rigida*. Further *Alchemilla vulgaris* and *Sibbaldia* were intermixed with the dwarf willow covering, but these plants also formed dense growths on damp spots rich in humus. The common heath plants *Dryas*, *Empetrum*, and *Juncus trifidus* occurred in very small quantity. But this composition of the species varies somewhat according to the varying degree of moisture of the soil. Thus, on a cold and damp slope with a north-eastern exposure, where the turf was chiefly formed of *Salix herbacea*, in addition to many of the above-mentioned plants I noted the following: *Cerastium trigynum*, *Ranunculus pygmaeus* (in several places these two latter species are found as associates), *Saxifraga stellaris*, *Veronica alpina*, *Epilobium alpinum*, all in quantity; further *Taraxacum officinale*, *Equisetum variegatum*, and *Alchemilla alpina*."

On pp. 194—195: "the three latter (*Gnaphalium norvegicum*, *G. supinum*, and *Sibbaldia procumbens*) occurred here and there in small depressions and grooves in such quantity that they formed

a continuous carpet." The three species referred to are some of the most typical plants of the snow patches in Iceland.

The above-cited descriptions of localities in connection with the flora lists given correspond closely to the geiri vegetation elsewhere, e. g. on Lýngdalsheiði and Arnarvatnsheiði, and even though Stefnásson does not distinguish the geiri or snow patch vegetation as a separate type, its presence in the highland tracts around Vatnadalur may be taken for granted. Hence the vegetation here consists of the following four types: mellar, mo, myri, and geiri.

The highland vegetation of East Iceland and Snæfellsnes has been described in more detail by Helgi Jónsson. In "Vegetationen paa Snæfellsnes", where the highland vegetation is dealt with, Helgi Jónsson distinguishes between 3 types, viz. grimmia heath, mountain pools, and fell-field ("Fjeldmark").

Of the fell-field we find the following statement on p. 27 ff.: "the fell-field, as taken here, extends over the upper region of the mountain from the upper limit of the heather moor at c. 300—400 m. above the sea, to the snow line, with the exception of the mountain pools and the grimmia heath." "Its surface is very heterogeneous, consisting now of extensive gravelly or gravelly and clayey flats, now of more or less downward sloping stretches, bare rocks and screes. In smaller hollows the subsoil is covered with layers of clay, and in depressions lakes of greatly varying sizes are met with."

"The plants of the fell field are scattered here and there, either in solitary specimens at a considerable distance from each other, or they are collected in small scattered tufts. Often they occur in patches, forming a carpet, notably the mosses, *Salix herbacea* and *Sibbaldia*. The scattered plants and the scattered patches of growth do not, however, affect the physiognomy of the landscape. What characterises the fell field is principally the stony, gravelly, or clayey soil."

"The vegetation of the fell field is very heterogeneous since, as was pointed out, the soil is very varied. As regards the appearance of the vegetation, the factors of decisive importance, besides the height above the sea, are the greater or less exposure of the locality and its water supply."

"The part played by the phanerogams in the composition of the vegetation grows less and less with increasing height; at the lower limit of the fell field on the other hand, they are very abundant. Here small *Empetrum* are met with in patches, *Loiseleuria*, *Cassiope*,

opeta, *Saliceta (herbacea)* and *Sibbaldieta* in irregular and confusing intermixture. Interspersed among them there are many herbs which do not belong to the fell field, especially the herbs of the heather moor. There is no well-marked limit here, but the fell field may be plainly distinguished by the fact that the plants of the heather moor are not able to form any heath but grow in patches or as scattered specimens, and that the small characteristic *Saliceta (herbacea)* and *Sibbaldieta* of the fell field have begun to appear."

H. Jónsson distinguishes between the following 5 types of vegetation in the fell field: gravelly flats, screes, the Anthelia-crust, the *Salix herbacea* and *Sibbaldia* vegetation, and the *Philonotis fontana* dy.

I. The gravelly flats. "With the exception of the naked rocks, the gravelly flats are those parts of the fell-field which are poorest in vegetation. In the upper part of the fell-field they are exceedingly poor in plants, especially if they are exposed; in the lower part of the exposed flats often only a solitary *Ranunculus glacialis* or a solitary *Cerastium alpinum* is met with. On less exposed flats in the lower part of the fell-field a considerably richer vegetation is met with." In such a locality *Salix herbacea* and *Alchemilla alpina* occurred in patches, further *Armeria*, *Aira alpina*, *Luzula spicata*, *Oxyria digyna*, *Cerastium alpinum*, *Silene acaulis*, *Arabis petraea*, *Galium silvestre*, and *Saxifraga cæspitosa*.

"On the gravelly flats which are studded with small shelter-givers, small stones dispersed more or less closely over the flat, we meet with the richest vegetation which can occur on a gravelly flat in the fell-field. Round the little stones there occur narrow fringes of *Grimmia hypnoides*. In the *Grimmia* fringes grow the most frequently occurring plants of the fell-field.

II. The screes. "From the last-mentioned gravelly flats there occur the smoothest transitions to the screes. When the shelter-givers, the scattered stones, become larger and occur closer together, the surface loses the character of a gravelly flat and must be regarded as a scree with small stones. Here *Grimmia hypnoides* is the most important plant, though it does not form heath." "As regards the plants intermixed with it, we must distinguish between the upper and the lower fell-field, or levels above and below 600 m."

In the upper fell field there is as a rule only an intermixture of lichens, the phanerogams are poorly represented. "Thus, in the upper part of the fell-field on Snæfellsnes Jökull at an altitude of 600 m. only the following species were met with: *Armeria maritima*,

Silene acaulis, *Luzula arcuata*, *Arabis petræa*, *Aira alpina*, *Oxyria digyna*, *Salix herbacea*, and *Saxifraga rivularis*." "At higher levels only some few individuals of *Salix herbacea*, *Sibbaldia procumbens*, and *Aira alpina* were met with."

"In the lower fell-field the phanerogams play a much more prominent part". The most frequent plants here are: *Salix herbacea*, *Saxifraga rivularis*, *Sibbaldia procumbens*, *Oxyria digyna*, *Ranunculus glacialis*, *Pedicularis flammea*, *Luzula arcuata*, and *Epilobium angustifolium*.

"The following occur frequently: *Silene acaulis*, *Carex rigida*, *Polygonum viviparum*, *Empetrum nigrum*, *Loiseleuria procumbens*, *Cassiope hypnoides*, *Armeria maritima*, *Arabis petræa*, *Veronica alpina*, *Thalictrum alpinum*, *Luzula spicata*, *Juncus trifidus*, *Saxifraga cæspitosa*, *Alchemilla alpina*, *Cerastium alpinum*, *Aira alpina*, *Thymus Serpyllum*, *Saxifraga oppositifolia*, *Gnaphalium supinum*, *Cerastium trigynum*, *Poa glauca*."

"The less frequent are: *Betula nana*, *Dryas octopetala*, *Papaver radicatum*, *Salix glauca*, *Trisetum subspicatum*, *Poa alpina*, *Pyrola minor*, *Saxifraga nivalis*, *S. hypnoides*, *Galium silvestre*, *Ranunculus acer*, *Cystopteris fragilis*. Of rarer occurrence are: *Taraxacum lævigatum*, *Rumex acetosa*, *Rhodiola rosea*, *Carex lagopina*, *Potentilla verna*, *Luzula multiflora*, *Festuca ovina*."

III. The Anthelia crust. "On gravelly, clayey, or stony soil, in the mountains, at an altitude of 300—700 m., increasing with the height, a grey crust, dispersed in patches, is very often met with. It is formed exclusively of *Anthelia nivalis*. Interspersed with it I sometimes found *Grimmia hypnoides*, *G. ericoides* and *Salix herbacea*. This *Anthelietum* often borders on the *Salix herbacea* depressions. Transitional forms between the Anthelia and the *Salix herbacea* vegetation are occasionally found."

IV. The *Salix herbacea* and *Sibbaldia* vegetation.
". . . occupies the aforementioned depressions where the clayey strata cover the subsoil. The main dispersal of this vegetation lies between 300 and 600 m. above sea level. In the lower part there is often a strong admixture of the elements of the heather moor, and at an altitude of over 600 m. it passes into the moss vegetation. An undergrowth formed of mosses is nearly always present." "Very often it is formed of *Grimmia hypnoides* and occasionally of *Anthelia nivalis*." "Not a few of the phanerogams of the fell-field are interspersed in the *Salix* and *Sibbaldia* patches. As far as I could

see, the following species were exclusively associated with this vegetation: *Taraxacum laevigatum*, *Epilobium anagallidifolium*, *Carex lagopina*, *Gnaphalium supinum*, *Pirola minor*." "Of the two dominant species, *Salix herbacea* and *Sibbaldia procumbens*, *Salix herbacea* is found in the greatest proportion. They either occur as separate dominants, or they dominate together intermixed with one another, and then either in equal number or with preponderance of the one or the other."

V. The *Philonotis fontana* Dý. "On damp gravel and at small springs small cushions of *Philonotis fontana* occur. In these light-green cushions of moss some flowering plant is generally met with, *Cerastium trigynum* and *Saxifraga rivularis* especially show a predilection for these spots. These moss cushions correspond to the dy occurring at lower levels."

The second type of vegetation which H. Jónsson distinguishes is that of rock pools. 1900, p. 20 he writes: "Up the mountains, though not at very high levels, there occurs a characteristic vegetation met with near pools, the vegetation of the rock pools; these pools are especially *Eriophorum* pools where *E. angustifolium* is solely predominant. They are extremely poor in species, yet we may mention the occurrence of scattered *Carex rostrata*, *C. pulla*, and *C. alpina*."

The third type of vegetation is the *Grimmia* heath. We have previously dealt with this vegetation (p. 40) with the main result that it belonged to the higher regions of the country to the south and east of the jökull line. It was most abundantly developed in the foggy and rainy regions of East Iceland, decreasing to the westward, and being absent in the north. "In the lowlands and at the lower levels of the mountains it changes in time and gives place to other plant societies; as a rule many phanerogams and vascular cryptogams are intermixed with it. These decrease considerably with increasing height above the sea, and have almost entirely disappeared from the *Grimmia* heath of the highest levels (at c. 600—700 m.); there only solitary, very widely scattered, common fell-field plants are met with."

A comparison shows a great, but probably more apparent than real, difference between the vegetation schemata of the two authors. Stefánsson describes the following types: melar, mo, myri, and snow-patch, Helgi Jónsson: fell-field (with sub-divisions gravelly flats, screes, the Anthelia crust, the *Salix herbacea* and *Sibbaldia*

vegetation, and the *Philonotis* dý), rock pools and *Grimmia* heath. Since the *Grimmia* heath does not occur in North Iceland, this type may be left out of consideration, and of the remainder only the myri and the rocky pools are identical. Judging from the description, H. Jónsson's fell-field comprises Stefánsson's melar, mo, and snow-patch, gravelly flats and screes corresponding to melar and mo, while the *Anthelia* crust and the *Salix herbacea* and *Sibbaldia* vegetation must be regarded as snow patch vegetations. Thus for the highlands we get the following vegetation scheme which, in its main lines, is the same as on Lýngdalsheiði, viz. 1) melar (and, in addition, for South and East Iceland, *Grimmia* heath), 2) mo, 3) myri (including dý), and snow-patch (including the *Salix herbacea* and *Sibbaldia* vegetation and the *Anthelia* crust). In the following each of these types will be dealt with in more detail.

As previously mentioned, the investigations to be described in the following were carried out on Arnarvatnsheiði. The latter forms part of the large plateau north-west of Langjökull which divides the Húna Flói area of valleys in the north from the Borgarfjörður area of valleys to the south. The surface of the plateau consists of deposits of the glacial period and appears as a landscape with countless downs, depressions, and lakes.

Of more conspicuous types of vegetation we find: melar, *Betula nana* mo, the knolly mo, jaðar, myri and flói, and geiri. The melar vegetation attains development at the top and on the ridges of the downs, occasionally some distance down the slopes. The *Betula nana* mo (or the level mo) occurs on large flats at high levels among tracts of melar. The mo (the knolly mo) occurs in small hollows in the *Betula nana* mo, along the slopes of the downs, in large flat depressions at high levels, and in the margins of the snow patches. Jaðar occurs especially in the depressions between the downs and on the borders of the myrar, while the myri vegetation occurs in the larger and deeper depressions and around the lakes. The moister parts of the myri are occupied by the flói. The geiri vegetation attains its finest development in large shovel-formed depressions in the hills, most frequently, though not so typically, developed along the slopes of the hills.

As elsewhere in Iceland, the melar and geiri vegetations are dependent respectively on a slight and a deep snow-covering. The

series: mo, jaðar, myri, and flói depends on the increasing content of moisture in the soil. In the following I shall describe the physiognomic, biological, and floristic relations of the individual types of vegetations.

The Melar Vegetation. Cf. figs. 15—17 and table 22 A, 1—6.

As mentioned above, the melar vegetation occurs at the top and on the ridges of the moraine walls. In the winter, when the landscape is covered with snow, these are either bare or have a very slight snow-covering. Consequently the frost penetrates deeper into the earth which again causes a slower process of thawing in the spring. This in connection with the position causes solifluction from the ridge of the hill towards the depression. On a steep slope the material will pour down in large tongues, as seen in fig. 23; if the slope is less steep, it will arrange itself in small ledges with a naked, gravelly horizontal surface, outwardly bounded by an edge covered with plants which connects the two corners of the ledge like a sweeping garland. Looking towards the depression, such an area of solifluction looks very poor in plants (cf. fig. 16), looking towards the ridge of the hill, the same surface seems somewhat more clothed with plants (cf. fig. 17).

The characteristics of melar are thus a slight or no snow-covering, solifluction, and a bare gravelly or stony soil.

The composition of the melar vegetation has been given in table 22 A, 1—6. Despite the open vegetation a relative abundance and density of species occur. The average number of species is 27, the density c. 8, varying from 5.6 to 9.4. In the biological spectrum the chamaephytes dominate with an average percentage of 52.4, H and especially G are relatively less important. The Th percentage is c. 2. Even if this figure is low, it is comparatively high compared with the Th percentage of the south country, a fact which it seems natural to connect with the relatively continental climate of the highlands. On melar in the north country the Th percentage is still higher; here the climate not only tends to be more continental than in the south country, but is also milder than in the highlands.

The A and E species are as 4 to 1; within the A sub-groups A 3 is especially conspicuous, the average percentage being 55.4. Of the E sub-groups only E 4 occurs and with a somewhat lower percentage than in the other types of vegetation.

Of plants which are characteristic, that is to say, which either occur here exclusively or occur here with the greatest F.-percentage, or which are comparatively frequent on melar, we may mention the following chamaephytes: *Thymus serpyllum*, *Cerastium alpinum*, *Arabis petraea*, *Minuartia verna*, *Arenaria ciliata*, *Saxifraga caespitosa*, and *S. oppositifolia*, *Dryas octopetala*, *Empetrum nigrum*, *Salix herbacea*, and *Silene acaulis*. Of hypogeophytes we mostly meet with grasses and cyperaceous plants. The following species occur: *Poa glauca*, *Festuca ovina*, *Juncus trifidus*, *Luzula arcuata*, and *L. spicata*, further *Polygonum viviparum*. Of species found exclusively on melar and thus characteristic of this type, we may mention *Arabis petraea*, *Luzula arcuata*, *Saxifraga caespitosa* and *S. oppositifolia*. Of therophytes only *Euphrasia latifolia* occurs.

The Betula nana mo. Cf. fig. 18 and table 22 A, 7—11.

This type of vegetation, provisionally named after its dominant chamaephyte, *Betula nana*, and referred to the mo on account of its comparatively close carpet of vegetation, occurs especially in large flat stretches among tracts of melar. The surface is not knolly as in the typical mo, nor does solifluction occur in any appreciable degree, as in melar. In small hollows in the *Betula nana* mo (the level mo), we meet with the knolly mo, which would seem to indicate a comparatively low degree of moisture in the soil of the *Betula nana* mo. Its distribution points to a snow-covering intermediate between the two types melar and knolly mo.

The vegetation is continuous, a feature which renders the *Betula nana* mo physiognomically very different from melar. The number and density of species are, however, not very much higher than in melar, the number of species being 32, the density 11.3, varying from 10.4 to 13.0. In the biological spectrum Ch are still dominant, even though the Ch percentage is reduced from 52 to 47. The reduction of the Ch percentage has resulted in an increase in the G percentage from 9.9 to 15.2. The species group spectrum shows a similar change; the A percentage has been reduced from 81 to 70, the A 3 percentage from 55 to 43, while, on the other hand, the A 2 percentage has risen. The increase of the E percentage falls practically only to E 4, which shows a percentage of 29 against 19 in the melar vegetation. The E 3 group only occurs with a percentage of 0.8.

The difference between melar and the *Betula nana* mo is most striking in a floristic respect, as even a hasty glance at table 22 A

TABLE 22 A.

The Melar and *Betula nana* Mo Vegetation on Arnarvatnsheiði.

Localities 1–6 represent the melar vegetation, 7–11 the *Betula nana* mo. All localities situated near Úlfsvatn c. 500 m. above sea level. No. 1 examined on $\frac{4}{8}$ 1925, 2 and 7 on $\frac{5}{8}$, and 8 on $\frac{6}{8}$; 4 and 9 on $\frac{7}{8}$, 5–6 and 10–11 on $\frac{8}{8}$ 1925. (25. $\frac{1}{10}$ m²).

TABLE 22 A. CONTINUED.

			1	2	3	4	5	6	7	8	9	10	11
Pedicularis flammea.....	A 3	H	»	»	»	4	»	»	»	16	»	»	4
Pingvicia vulgaris.....	E 4	H	12	»	»	8	»	»	20	»	»	»	»
Rumex acetosa.....	E 3	H	»	»	»	»	»	»	»	»	»	»	4
Salix lanata.....	A 1	Ch	»	»	»	»	»	»	4	»	»	»	»
Saxifraga Hirculus	A 3	H	»	»	»	»	»	»	»	4	»	»	»
Sedum villosum.....	A 2	H	8	12	»	4	4	»	»	»	»	»	»
Tofieldia palustris.....	A 2	H	12	»	»	»	»	»	48	»	8	»	»
Trisetum spicatum.....	A 3	H	12	16	»	12	4	»	36	»	»	12	8

TABLE 22 B.

Biological Spectra of the Melar and Betula nana Mo.

	1	2	3	4	5	6	7	8	9	10	11
Points sum.....	936	792	560	848	812	800	1304	1044	1064	1172	1080
Number of species ..	34	31	20	32	24	21	36	32	29	29	32
Density of species ..	9.4	7.9	5.6	8.5	8.1	8.0	13.0	10.4	10.6	11.7	10.8
A.....	79.1	81.8	81.4	79.2	83.3	80.0	71.5	73.6	68.4	71.7	66.3
E.....	20.9	18.2	18.6	20.8	16.7	20.0	28.5	26.4	31.6	28.3	33.7
A 3	51.3	59.1	56.4	55.7	59.1	50.5	40.5	47.5	41.4	44.7	40.0
A 2	24.4	18.7	12.9	21.7	19.7	22.5	27.6	24.1	25.6	21.8	22.2
A 1	3.4	4.0	12.1	1.9	4.4	7.0	3.4	1.9	1.5	5.1	4.1
E 4	20.9	18.2	18.6	20.8	16.7	20.0	27.6	26.4	30.8	26.6	33.3
E 3	»	»	»	»	»	»	0.9	»	0.8	1.7	0.4
E 2	»	»	»	»	»	»	»	»	»	»	»
E 1	»	»	»	»	»	»	»	»	»	»	»
Ch.....	50.0	49.0	59.3	53.3	53.2	49.5	46.6	45.2	49.2	47.4	47.8
H	37.6	36.4	31.4	34.0	36.5	39.5	40.8	36.0	33.5	39.9	33.3
G	10.7	9.1	8.6	11.8	8.4	10.5	11.7	17.2	16.9	12.6	17.8
HH.....	»	»	»	»	»	»	»	»	»	»	»
Th.....	1.7	5.6	0.7	0.9	2.0	0.5	0.9	1.5	0.4	»	1.1

will show. Some species occur exclusively or principally on melar, others exclusively or principally in the *Betula nana* mo, while a third group is common to both types of vegetation. The table shows more precisely which species belong to the respective groups. Physiognomically the chamaephytes dominate. A random selection of

the more conspicuous species includes: *Empetrum nigrum*, *Salix herbacea*, *S. glauca*, *Betula nana*, *Vaccinium uliginosum*, *Dryas octopetala*, *Silene acaulis*, and *Armeria vulgaris*. The species *Cassiope hypnoides* and *Loiseleuria procumbens* occur more frequently than in melar even though they are not as dominant as in the knolly mo.

Of hemicryptophytes and geophytes the following occur: *Polygonum viviparum*, *Juncus trifidus*, *Luzula spicata*, *Festuca ovina*, *Viscaria alpina*, *Galium Normanni*, *Thalictrum alpinum*, *Elyna Bellardi*, *Carex rigida*, *Festuca rubra*, and *Poa alpina*. Of pteridophytes *Selaginella selaginoides*, *Equisetum arvense*, and *E. variegatum* are met with.

Along the upper margin of the large snow patches there occurs a narrow belt in which *Betula nana* is the physiognomic dominant. This formation will be dealt with later, under the geiri vegetation.

The Knolly Mo. Cf. fig. 19 and table 23 A, 1—5.

This type of vegetation commonly occurs on flat sheltered slopes, on the lower slopes of elevations and ridges with melar above, in small hollows in the *Betula nana* mo, and on the borders of the snow patches. The surface is always knolly, but the knolls are neither very large nor very high. Judging by the position the snow-covering is deeper than in the two preceding types, the melar and the level mo, though less deep than in the snow patches. As regards moisture, the knolly mo occupies an intermediate position between the level mo and the jaðar vegetation.

The change in number of species and in density is continued from melar through the level mo to the knolly mo and here we have the values 35 and 15 respectively for the number of species and the density. Biologically the change is likevise continued: the Ch percentage has decreased, while the G and H percentages have increased. The E and A percentages have remained constant, while there is still a decrease in the A 3 percentage. There is a rise in the E 3 percentage.

While in the *Betula nana* mo Ch were dominant and H were the subordinate element, the reverse is the case in the knolly mo. Here H are the dominant. The respective averages for Ch and H in the two types of vegetation are 47:38 and 37:47.

The predominant chamaephytes are *Empetrum nigrum*, *Vaccinium*, and *Salix herbacea*. In more scattered growth there occur *Salix glauca*, *Silene acaulis*, *Armeria vulgaris*, *Dryas octopetala*, *Thy-*

TABLE 23 A.

The Mo and Jaðar Vegetation on Arnarvatnsheiði.

Localities 1—5 represent the mo vegetation, 6—10 the Jaðar vegetation. All localities situated near Úlfsvatn c. 500 m. above sea level. 1, 2, 5 examined on $\frac{5}{8}$ 1925; 8 on $\frac{9}{8}$, 3 and 6 on $\frac{12}{8}$, 4 and 9 on $\frac{13}{8}$, 7 and 10 on $\frac{14}{8}$ 1925. (7, 10. $\frac{1}{10}$ m²; 1—6, 8—10, 25. $\frac{1}{10}$ m²).

			1	2	3	4	5	6	7	8	9	10
Dryas octopetala	A 3	Ch	28	8	40	52	»	»	»	»	»	»
Thymus serpyllum	E 4	Ch	20	»	24	12	»	4	»	»	»	»
Cassiope hypnoides.....	A 2	Ch	20	76	20	48	36	»	»	»	»	»
Loiseleuria procumbens..	A 2	Ch	12	36	32	16	12	»	»	»	»	»
Elyna Bellardi	A 3	H	68	24	76	56	»	16	»	»	8	4
Juncus trifidus.....	A 2	H	56	40	60	64	20	20	10	»	4	»
Selaginella selaginoides ..	A 1	Ch	80	72	76	72	32	16	»	»	4	4
Agrostis canina	E 3	H	76	60	48	12	4	28	»	»	»	4
Trisetum spicatum	A 3	H	20	40	56	16	4	»	»	4	»	»
Tofieldia palustris.....	A 2	H	16	44	4	16	4	8	»	4	»	»
Viscaria alpina	A 2	H	12	8	28	20	»	4	»	»	»	»
Bartschia alpina	A 2	H	16	56	28	36	28	16	»	12	»	»
Empetrum nigrum	E 4	Ch	100	100	96	96	96	36	»	52	40	8
Vaccinium uliginosum...	E 4	Ch	80	76	92	44	68	8	»	»	20	8
Luzula spicata	A 2	H	68	68	56	68	52	36	10	32	32	44
Silene acaulis	A 3	Ch	40	64	48	60	36	36	»	16	12	20
Equisetum variegatum..	A 3	H	76	88	92	60	64	64	10	4	48	60
Salix herbacea	A 3	Ch	88	100	84	76	88	84	»	44	60	100
— glauca.....	A 3	Ch	20	24	32	48	60	56	20	48	48	44
Armeria vulgaris	A 3	Ch	16	8	20	44	12	28	»	8	16	16
Polygonum viviparum ..	A 3	G	96	100	92	92	100	92	70	96	96	100
Thalictrum alpinum.....	A 2	H	88	88	96	88	80	100	70	92	80	88
Carex rigida	A 3	G	44	96	60	52	100	100	90	96	100	100
Festuca rubra.....	E 4	H	92	96	88	100	64	96	70	68	44	40
— ovina.....	E 4	H	8	»	16	24	12	16	10	36	16	32
Poa alpina	A 2	H	20	40	40	48	4	64	»	16	16	40
— glauca.	A 3	H	4	20	16	8	4	20	»	4	8	12
Rumex acetosa	E 3	H	8	8	24	20	16	40	30	16	52	48
Galium Normannii	A 1	H	44	52	56	24	8	68	30	24	32	28
Cerastium alpinum.....	A 2	Ch	8	»	4	32	»	32	30	20	48	8
Equisetum arvense	E 4	G	16	12	»	80	80	80	60	76	80	96
Deschampsia alpina	A 2	H	»	»	»	»	4	8	»	40	32	44
Salix phyllicifolia	A 1	Ch	»	8	»	»	»	24	30	24	36	8
Cardamine pratensis....	E 4	H	»	»	»	»	48	20	60	64	80	76
Taraxacum officinale ..	E 2	H	»	»	»	»	»	16	80	28	24	16
Potentilla verna	A 2	H	»	»	»	»	»	24	80	24	24	24
Poa pratensis	E 4	G	»	»	»	»	»	»	90	»	32	24
Agrostis tenuis	E 2	H	»	»	»	»	»	»	»	4	»	»
Alchemilla minor	E 4	H	»	»	»	»	»	»	40	»	»	»

TABLE 23 A CONTINUED.

			1	2	3	4	5	6	7	8	9	10
Anthoxanthum odoratum.	E 3	H	2	»	»	»	»	4	»	»	4	4
Betula nana	A 2	Ch	2	4	»	»	»	»	»	4	4	-
Botrychium Lunaria....	E 4	G	4	8	4	4	»	»	»	»	»	»
Calamagrostis neglecta...	E 4	H	»	»	»	»	16	»	10	»	32	32
Carex alpina.....	A 2	H	2	»	»	»	»	»	»	4	4	8
— dioica	E 4	G	»	»	»	»	4	»	»	»	»	12
— Goodenoughii	E 3	G	»	»	»	»	4	2	»	»	»	»
— rariflora	A 2	G	»	»	»	»	»	»	»	4	8	4
Cerastium trigynum	A 2	Ch	2	»	»	»	»	»	40	»	»	»
Deschampsia flexuosa....	E 3	H	12	8	4	4	»	12	40	»	»	»
Draba rupestris	A 1	Ch	»	»	»	»	»	4	40	»	»	4
Equisetum pratense	E 2	G	»	»	»	»	»	8	»	»	20	»
Eriophorum polystachyum	E 4	G	»	»	»	»	»	»	»	48	16	8
Euphrasia latifolia	A 2	Th	»	12	»	»	»	»	»	12	4	24
Gentiana nivalis	A 2	Th	»	»	»	»	»	»	»	4	»	»
— tenella.....	A 2	Th	»	4	4	»	»	»	20	»	»	4
Hieracium alpinum	A 2	H	»	»	4	»	»	»	»	»	»	»
Koenigia islandica.....	A 3	Th	»	»	»	»	»	»	10	8	»	»
Luzula arcuata.....	A 3	H	»	»	4	»	»	»	»	»	»	»
— multiflora	E 3	H	»	»	»	»	»	4	»	»	12	»
Minuartia biflora	A 3	Ch	»	»	4	»	4	»	»	4	»	»
— verna	A 3	Ch	4	»	»	16	»	»	»	»	»	»
Pedicularis flammea.....	A 3	H	»	4	»	»	12	»	»	16	»	»
Phleum alpinum	A 2	H	»	»	»	»	»	4	40	»	16	4
Pingvicia vulgaris	E 4	H	4	20	»	12	8	4	»	»	»	»
Ranunculus acer	E 4	H	»	»	»	»	»	»	30	»	»	»
Salix lanata	A 1	Ch	»	»	»	»	»	»	»	12	4	»
Saxifraga Hirculus.....	A 3	H	»	»	»	»	16	4	»	16	8	»
Sedum villosum	A 2	H	»	»	»	»	»	»	»	4	»	»
Sibbaldia procumbens ...	A 2	Ch	»	»	»	»	»	»	10	»	»	»
Veronica alpina	A 2	H	»	»	»	»	»	»	10	»	»	8
Viola palustris	E 3	H	»	»	»	»	»	»	40	»	4	»

mus serpyllum, *Cassiope hypnoides*, and *Loiseleuria procumbens*. For the rest grasses and cyperaceous plants dominate, thus *Elyna Bellardi*, *Juncus trifidus*, *Luzula spicata*, and *Carex rigida*, further *Festuca rubra*, *F. ovina*, *Agrostis canina*, *Trisetum spicatum*, *Deschampsia flexuosa*, *Poa alpina* and *P. glauca*. Of herbaceous plants we find especially *Polygonum viviparum* and *Thalictrum alpinum*; less dominant plants are *Tofieldia palustris*, *Rumex acetosa*, *Viscaria alpina*, *Bartschia alpina*, *Galium Normanni*, and *Pinguicula vulgaris*. Pteridophytes are represented by *Selaginella selaginoides*, *Equisetum*

TABLE 23 B.

Biological Spectra of the Mo and Jaðar Vegetation.

	1	2	3	4	5	6	7	8	9	10
Points sum	1364	1572	1528	1520	1200	1304	1180	1084	1232	1208
Number of species..	35	36	36	35	35	40	30	38	42	39
Density of species..	13.6	15.7	15.3	15.2	12.0	13.0	11.8	10.8	12.3	12.1
A	69.2	75.2	74.1	73.2	65.0	71.2	52.5	64.2	61.0	66.2
E	30.8	24.7	25.9	26.8	35.0	28.8	47.5	35.8	39.0	33.8
A 3.....	37.5	36.6	41.1	40.3	41.7	40.8	19.5	35.4	36.7	38.4
A 2.....	22.6	30.3	24.3	26.7	20.0	21.8	24.6	23.2	18.2	24.2
A 1.....	9.1	8.4	8.6	6.3	3.3	8.6	8.5	5.5	6.2	3.6
E 4.....	23.8	19.8	20.9	24.5	33.2	20.2	31.4	31.7	29.2	27.8
E 3.....	7.0	4.8	5.0	2.4	2.0	6.7	9.3	1.5	5.8	4.6
E 2.....	»	»	»	»	»	1.8	6.8	2.6	3.9	1.3
E 1.....	»	»	»	»	»	»	»	»	»	»
Ch	37.8	36.6	37.4	40.5	37.0	25.1	14.4	21.4	23.7	17.9
H	50.4	48.6	52.1	44.5	39.0	53.4	57.6	46.9	47.4	51.0
G	11.7	13.7	10.2	15.0	24.0	21.5	26.3	29.5	28.6	28.5
HH	»	»	»	»	»	»	»	»	»	»
Th	»	1.0	0.3	»	»	»	2.5	2.2	0.3	2.3

variegatum, and *E. arvense*. *Botrychium Lunaria* occurs singly but constantly.

Thus to the above-mentioned physiognomic and biological differences between the level and the knolly mo must be added the following floristic differences: *Salix glauca* and *Betula nana* occur exclusively in the level mo. With a lower F.-percentage in the knolly mo we meet with *Festuca ovina*, *Minuartia verna*, *Silene acaulis*, and several others. Predominantly occurring in the knolly mo, we find: *Loiseleuria procumbens*, *Agrostis canina*, *Trisetum spicatum*, *Poa alpina*, *Deschampsia flexuosa*, *Carex rigida*, *Rumex acetosa*, *Selaginella*, *Equisetum variegatum*, *Bartschia alpina* and several others.

The two types of mo must thus be said to be well distinguished.

The Jaðar Vegetation. Cf. fig. 20 and table 23 A, 6—10.

In depressions between the moraine walls, on the borders of the mýrar, in small damp hollows in the mo, and as a fringe along the rivers the jaðar vegetation is met with. When typically deve-

loped it is easily distinguished from the other types of vegetation by the very large knolls of which the surface consists. These often attain a height of 1 m. or more and 1 or several m in diameter. The distance between the individual knolls is up to $\frac{1}{2}$ m. The jaðar vegetation belongs to moderately damp soil having a normal snow-covering in the winter. The composition of the vegetation can be shown to differ somewhat in the different localities, and possibly several types of highland jaðar may with good reason be established in the future, according to the degree and kind of moisture of the soil, and the amount of shelter provided by the snow-covering.

On an average, the density of species was c. 12, the number of species 35, in the jaðar localities examined by me. Ch have become much less dominant, the Ch percentage is only 20.5 and attains a relative minimum with this value, whereas the H percentage attains its maximum here, the average H percentage being 51.3. The G percentage which has risen steadily has reached a value of 27; it is noteworthy that the Th percentage attains a relative maximum of 1.5 in the jaðar vegetation.

The peculiarities to be noted in the species group spectrum are a diminution of the A percentage due in the main to a diminution of the A 3 percentage, a slight rise in the E 3 percentage, and the appearance of E 2 species in a quantity of 3.3 per cent.

The more conspicuous chamaephytes are *Empetrum nigrum* and the *Salix* species *Salix herbacea*, *glauca*, and *phylicifolia*; *Salix phylicifolia* is the characteristic dominant for jaðar. In more scattered growth there occur *Vaccinium uliginosum*, *Silene acaulis*, *Armeria vulgáris*, and *Cerastium alpinum*. For the rest it is H and G which characterise the vegetation, notably *Carex rigida*, and in addition, on the wettest soil, *Deschampsia alpina*. The more prominent species are *Polygonum viviparum*, *Thalictrum alpinum*, *Luzula spicata*, *Carex rigida*, *Equisetum arvense*, *E. variegatum*, *Festuca rubra*, *F. ovina*, *Deschampsia alpina*, *Poa alpina*, *Rumex acetosa*, *Galium Normannii*, *Cardamine pratensis*, *Taraxacum officinale*, *Potentilla verna*, *Poa pratensis*, *Calamagrostis neglecta*, *Viola palustris*, and *Saxifraga Hirculus*. A number of these species are characteristic of the jaðar.

A couple of types which I had not time to examine more closely shall be briefly mentioned here. One is the moss mo which St. Stefánsson has described from Grimstungnaheiði (1894, p. 201 (cf. p. 10)). This type of vegetation was also found on Arnarvatns-

heiði, and there it seemed to be peculiar to hollows, the bottom of which consisted of large boulders over which *Grimmia* had spread a deep dense carpet with scattered specimens of *Carex rigida*, *Pedicularis flammea*, *Saxifraga Hirculus* and several others.

The other type is the jaðar along the banks of rivers. Physiognomically it resembles the jaðar further inland, but floristically it differs from it by the fact that a number of species such as *Carex Goodenoughii*, *Caltha palustris*, *Geum rivale*, *Comarum palustre*, and *Menyanthes trifoliata* either exclusively or practically exclusively occur here, and that merely as a narrow fringe only few metres wide along both sides of the stream. Since in the lowlands the species occur both in the myri far from running water and along streams, their predilection for streams in the highlands cannot be due to any general property of these, such as an abundance of nourishment and oxygen, but must be referred to other causes. Since all the aforementioned plants are southern species, and since the presence of water in the highlands also otherwise favours the southern species, it seems natural to suppose that the more abundant occurrence of more southern plants in immediate association with running water is due to the fact that running water warms the soil more than stagnant water even though water in all cases acts as a reservoir of heat.

The Mýri and Flói Vegetation. Cf. figs. 21—22 and table 24 A, 1—13.

The myri vegetation occurs in the dampest hollows and especially around the numerous lakes. A depression with myri has the following appearance. On somewhat damper ground than the above-described jaðar with the large knolls, there occurs a Carex myri with small knolls. The damper central parts have a level surface without knolls and consist of a mosaic of formations which are fairly distinct and visible at a distance by the different tinges they communicate to the landscape. The knolly Carex myri may send out darker stripes into the myri, while the level myri itself consists of yellowish-green patches with *Carex rostrata* as the dominant, white patches in which *Eriophorum polystachyum* in fruit dominates, brown patches with *Carex rariflora*, and smaller or larger collections of water.

According to the degree of moisture of the soil, three zones of moisture may be distinguished; the knolly Carex myri on the least

TABLE 24 A. The Mýri and Flói Vegetation on Arnarvatnsheiði.

Localities 1–4 represent the driest myri nearest the jaðar, 5–9 the moister myri passing into flói outwards, 10–13. Localities 1, 2, 5, 6, 7, 13 examined on $^9/8$ 1925; 8, 11, 12 on $^{10}/8$, 10 on $^{12}/8$, 3, 4, 9 on $^{14}/8$ 1925.
 $(25 \cdot 1/10 \text{ m}^2)$.

TABLE 24 B.

Biological Spectra of the Mýri and Flói Vegetation.

	1	2	3	4	5	6	7	8	9	10	11	12	13
Points sum	944	768	840	840	436	404	496	504	504	276	196	212	248
Number of species ..	23	27	22	20	11	10	10	13	12	5	8	10	6
Density of species ..	9.4	7.7	8.4	8.4	4.4	4.0	5.0	5.0	5.0	2.8	2.0	2.1	2.5
A	51.3	64.1	55.2	53.8	67.9	66.3	70.2	65.1	62.7	7.2	49.0	45.3	38.7
E	48.7	53.9	44.8	46.2	32.1	33.7	29.8	34.9	37.3	92.8	51.0	54.7	61.3
A 3	35.2	49.0	49.0	37.6	25.7	40.6	36.3	42.9	20.6	7.2	20.4	41.5	11.3
A 2	14.0	13.5	5.7	13.3	22.9	24.8	20.2	19.8	19.8	»	10.2	1.9	27.4
A 1	2.1	1.6	0.5	2.9	19.3	1.0	13.7	2.4	22.2	»	18.4	1.9	»
E 4	48.7	35.9	43.8	44.7	30.3	33.7	10.5	34.9	37.3	49.3	51.0	54.7	54.8
E 3	»	»	1.0	1.4	1.9	»	19.4	»	»	43.5	»	»	6.5
E 2	»	»	»	»	»	»	»	»	»	»	»	»	»
E 1	»	»	»	»	»	»	»	»	»	»	»	»	»
Ch	26.7	27.1	23.3	32.9	10.1	19.8	16.9	15.9	7.9	»	14.3	5.7	4.8
H	26.7	28.6	31.0	16.7	8.3	8.9	11.3	13.5	13.5	13.0	»	32.1	14.5
G	45.7	43.8	45.2	48.6	79.8	71.2	52.4	70.6	78.6	79.7	85.7	62.3	74.2
HH	»	»	0.5	1.4	1.8	»	19.4	»	»	7.2	»	»	6.5
Th	0.8	0.5	»	0.5	»	»	»	»	»	»	»	»	»

damp soil, the Carex rariflora mýri on damper soil, and the Eriophorum polystachyum flói on the dampest ground. In table 24 A, Nos. 1—4 represent the knolly mýri, 5—9 the Carex rariflora mýri, and 10—13 the flói.

The knolly Carex mýri is most abundant in species and shows the greatest density of species of the mýri formations. The number of species is 23, and the density 8.5. Ch play a more prominent part here than in the jaðar and attain a relative maximum of 27.5 per cent. H show a strong decrease, while the rise in G is still continuing; the last Th meet with the first HH. The species group spectrum shows a large content of A 3 and E 4 species.

The physiognomic dominants are the chamaephytes and the Cyperaceæ, of the chamaephytes especially *Salix herbacea*, *S. glauca*, and *S. phyllicifolia*, further *Empetrum nigrum* and *Vaccinium uliginosum*, of the Cyperaceæ *Eriophorum polystachyum*, *Carex rigida*, *C. dioica*, *C. rariflora*, and here and there *Carex alpina* and *C. sax-*

atilis. Of more or less importance are *Polygonum viviparum*, *Calamagrostis neglecta*, *Equisetum arvense* and *E. variegatum*, *Cardamine pratensis*, *Thalictrum alpinum*, *Luzula spicata*, *Festuca ovina*, *F. rubra*, and *Saxifraga Hirculus*.

The Carex rariflora Mýri. Cf. fig. 22 and table 24 A, 5—9.

On still damper ground the knolls disappear and with them a number of species, so that the species now only number 11.2, while the density of species is 4.7. The geophytes, comprising especially Cyperaceæ, form the bulk of the vegetation. The G percentage is 70.5, the HH percentage 4.2, the Ch and H percentages 14.1 and 11.1 respectively. The species group spectrum shows the peculiarity of a rise in the A percentage from 56 to 66 caused by a great rise in the A 2 and A 1 percentages; the A 3 percentage, on the other hand, is still reduced. The dominant species are *Carex rariflora* and *Eriophorum polystachyum*, also, in spots, *Carex chordorrhiza* and *C. rostrata*. Other frequently occurring plants are *Polygonum viviparum*, *Salix glauca*, and *Cardamine pratensis*.

The Eriophorum polystachyum Flói. Cf. Table 24 A, 10—13.

On the flói, the dampest soil clothed with plants, knolls are likewise absent, the ground is swampy as in the lowland flói, and not firm enough to walk on. The succession of changes in number of species, density of species, biological spectrum and species group spectrum in the mýri formations here reaches its climax, as was also the case in the lowland flói.

The sole dominant here is *Eriophorum polystachyum*, here and there a few mýri plants occur such as *Carex rariflora*, *C. chordorrhiza*, *C. rostrata*, *C. saxatilis*, *Polygonum viviparum*, *Salix glauca*, and *Calamagrostis neglecta*.

The Geiri Vegetation. Cf. table 25 A, 1—6 and figs. 23—25.

On slopes with a southern, western, and northern exposure a special vegetation, the snow patch or geiri vegetation, may be met with. Its peculiarities are conditioned by a deep and constant snow-covering in the winter. The snow falls early on these areas, covers them without intermission throughout the winter, and only melts well on in the spring.

The snow patches occur in two different forms. Most frequently the snow lies in long narrow bands on the southern, western, and

northern slopes of the hills (cf. fig. 23), abutting above on the melar, whence the soil rolls down on to it, and passing below into the knolly mo. More rarely the snow patches occur in the shape of large depressions having the form of a parabola in the western and southern slopes of the hills. The shape of these large patches of snow is very characteristic; above they are separated from the melar by a narrow steep edge. The sides of the snow patch slope strongly above, are less steep further down, and finally pass into the bottom of the patch which as a slightly hollow surface slopes gently towards the mouth of the snow patch. The shape most of all resembles a large shovel dug into the slope. The bed of a rivulet extends some way into the patch. Outwardly this form, too, passes into the knolly mo.

The surface is level and without knolls in both forms of snow patch, as may be seen with sufficient plainness in the figures.

While the vegetation is uniform throughout the whole snow patch in the first type, differing only according to the exposure, a distinction can be drawn in large snow patches between a marginal zone, the vegetation on the sides, and a bottom vegetation. The vegetation is most characteristic in the large snow patches, a number of snow patch plants being exclusively found here, just as the marginal zone is a formation peculiar to the large snow patches. As regards the vegetation of the bottom, it seems to correspond to that of smaller snow patches with a northern exposure, while the vegetation of the sides corresponds to that of smaller snow patches with a southern exposure. Hence the floristic relations of the snow patches may be dealt with under one head, the following three formations requiring to be treated: 1) a marginal zone with *Betula nana*, and possibly *Juniperus communis*, 2) a Geranium belt comprising small patches having a southern or western exposure and the vegetation of the sides of the large snow patches, and 3) the bottom vegetation, which comprises, in addition, the vegetation of snow patches having a northern exposure. Table 25 A, 1—6 shows the circling results for the vegetation of the snow patches. No. 1 is the vegetation of the marginal zone, Nos. 2—4 the Geranium belt, and Nos. 5—6 the bottom vegetation. Nos. 1, 2—3, and 6 originate from the same large snow patch, 5 and 4 represent the smaller patches, respectively with a northern and a southern exposure.

TABLE 25 A. The Geiri Vegetation on Arnarvatnsheiði.

Locality 1 represents the marginal vegetation of the snow patch, 2—4 the vegetation on the sides of the snow patch, 5—6 the vegetation on the bottom of the snow patch. No. 2 examined on $^5/8$ 1925; 1, 3, 6 on $^6/8$, 4 on $^8/8$, 5 on $^9/8$ 1925. (25. $1/10$ m 2).

			1	2	3	4	5	6
Betula nana	A 2	Ch	72	»	»	»	»	»
Thymus serpyllum	E 4	Ch	48	»	»	12	»	»
Dryas octopetala	A 3	Ch	16	»	»	»	»	»
Silene acaulis	A 3	Ch	12	»	4	»	»	»
Armeria vulgaris	A 3	Ch	16	»	»	»	»	»
Juncus trifidus	A 2	H	24	»	8	8	»	»
Elyna Bellardi	A 3	H	12	»	»	4	»	»
Geranium sylvaticum	E 3	H	12	96	84	100	4	»
Vaccinium uliginosum	E 4	Ch	88	64	96	96	100	»
Salix herbacea	A 3	Ch	68	96	88	80	100	100
— glauca	A 3	Ch	52	64	56	44	84	92
— phylicifolia	A 1	Ch	8	56	28	16	12	»
Empetrum nigrum	E 4	Ch	92	68	68	88	100	»
Polygonum viviparum	A 3	G	76	84	52	68	64	44
Thalictrum alpinum	A 2	H	88	80	100	100	72	16
Carex rigida	A 3	G	80	72	92	88	92	76
Deschampsia flexuosa	E 3	H	72	96	96	100	92	56
Festuca rubra	E 4	H	76	60	12	44	48	76
Agrostis canina	E 3	H	24	68	16	80	80	96
Hierochloë odorata	E 2	G	4	56	8	20	20	12
Anthoxanthum odoratum	E 3	H	8	88	8	60	»	4
Selaginella selaginoides	A 1	Ch	20	16	16	56	»	»
Galium Normannii	A 1	H	56	8	8	68	»	»
— verum	E 1	H	20	12	28	52	»	»
Equisetum arvense	E 4	G	16	60	16	8	48	84
— variegatum	A 3	H	36	»	16	8	20	12
Rumex acetosa	E 3	H	12	32	44	4	4	64
Phleum alpinum	A 2	H	»	36	12	12	8	24
Ranunculus acer	E 4	H	»	44	28	4	»	20
Viola palustris	E 3	H	8	24	48	»	40	20
Taraxacum officinale	E 2	H	»	12	48	»	40	20
Agrostis tenuis	E 2	H	4	»	64	»	»	»
Alchemilla minor	E 4	H	»	20	16	4	»	»
Sibbaldia procumbens	A 2	Ch	»	36	»	»	»	44
Gnaphalium supinum	A 2	Ch	»	24	»	»	»	72
Alchemilla alpina	A 2	Ch	4	»	16	4	»	»
Betula alpestris	A 1?	Ch	»	»	»	4	»	»
Botrychium Lunaria	E 4	G	4	»	»	8	»	»
Calamagrostis neglecta ...	E 4	H	»	»	»	»	»	8

TABLE 25 A. CONTINUED.

		1	2	3	4	5	6
Cardamine pratensis	E 4	H	»	»	4	»	»
Deschampsia caespitosa	E 2	H	»	»	4	»	»
Festuca ovina	E 4	H	12	»	»	4	»
Gentiana nivalis	A 2	Th	»	»	»	8	»
Habenaria viridis	A 1	G	»	»	»	12	»
Hieracium alpinum	A 2	H	»	»	»	4	»
Leontodon autumnalis	E 3	H	»	»	»	»	12
Luzula spicata	A 2	H	20	8	»	»	»
Poa alpina	A 2	H	20	44	»	8	»
— glauca	A 3	H	»	4	»	»	»
Potentilla verna	A 2	H	»	»	»	12	»
Veronica alpina	A 2	H	»	»	4	»	»

TABLE 25 B. Biological Spectra of the Geiri Vegetation.

	1	2	3	4	5	6
Points sum	1180	1428	1192	1272	1004	996
Number of species	34	29	33	33	20	22
Density of species	11.8	14.3	11.9	12.7	10.0	10.0
A	57.6	44.0	41.9	46.5	46.2	49.4
E	42.4	56.0	58.1	53.5	53.8	50.6
A 3	31.2	22.4	25.8	23.0	35.9	32.5
A 2	19.3	16.0	11.7	11.3	9.2	16.9
A 1	7.1	5.6	4.4	12.3	1.2	»
E 4	28.5	22.1	20.5	20.8	29.9	18.9
E 3	11.5	28.3	24.8	27.0	17.9	28.5
E 2	0.7	4.8	10.4	1.6	6.0	3.2
E 1	1.7	0.8	2.3	4.1	»	»
Ch	42.0	29.7	31.2	31.4	39.4	30.9
H	42.7	51.3	54.7	51.9	38.2	47.4
G	15.3	19.0	14.1	16.1	22.3	21.7
HH	»	»	»	»	»	»
Th	»	»	»	0.6	»	»

The Marginal Zone.

Along the entire upper edge of the large snow patches there occurs a narrow belt, rarely more than 1—2 metres wide, where a

number of chamaephytes attain a luxuriant development. The dominant species are *Betula nana*, *Empetrum nigrum*, *Salix glauca* and *herbacea*, and *Vaccinium uliginosum*; in some snow patches one may likewise find *Juniperus communis* and *Betula alpestris*. All species attain a vigorous growth and form a dense mat of shrub-like vegetation. Beneath the chamaephytes there is a bottom layer formed of species like *Deschampsia flexuosa*, *Festuca rubra*, *Carex rigida*, *Polygonum viviparum*, *Thalictrum alpinum*, *Galium Normannii*, and a number of mo plants such as *Thymus Serpyllum*, *Dryas octopetala*, *Silene acaulis*, *Armeria vulgaris*, *Juncus trifidus*, *Elyna Bellardi*, *Luzula spicata* and several others.

The *Geranium silvaticum* Belt.

This formation initiates the snow patch vegetation proper. As stated above, it occurs on the steep sides of the large snow patches and in the smaller ones on slopes having a southern and western exposure.

H are considerably more dominant here than in the marginal zone whereas Ch are of minor importance. The most conspicuous plant is *Geranium silvaticum* (cf. fig. 25). Under this plant and mixed with it there occurs a dense vegetation of Ch and herbs: *Vaccinium uliginosum*, *Salix herbacea*, *S. glauca*, and *S. phyllicifolia*, *Empetrum nigrum*, *Polygonum viviparum*, *Thalictrum alpinum*, *Equisetum arvense*, *Carex rigida*, *Deschampsia flexuosa*, *Agrostis canina* and *A. tenuis*, *Festuca rubra*, *Hierochloë odorata*, *Anthoxanthum odoratum*, *Phleum alpinum*, *Poa alpina*, *Rumex acetosa*, *Ranunculus acer*, *Viola palustris*, *Taraxacum officinale*, *Galium verum*, *Alchemilla alpina*, and *A. minor*; and *Sibbaldia procumbens*.

The table shows more precisely the quantitative distribution of the individual species. In the main the three localities examined by me are in accordance even though some few species deviate. The deviations probably express differences of environment, but the material is so small that there is no reason for a more detailed discussion.

The Bottom Vegetation.

Covering the bottom of the snow patch, below the *Geranium* belt and well marked off from it, there occurs a *Salix glauca*-*Gnaphalium supinum* formation. This formation is somewhat poorer in species than the *Geranium* belt above. The density of

species is likewise less, 10.0 as against 14.3. The dominant or typical species are *Salix glauca*, *S. herbacea*, *Sibbaldia procumbens*, and *Gnaphalium supinum*. *Vaccinium uliginosum*, *Empetrum nigrum*, and *Salix phylicifolia* have entirely disappeared. Of more or less dominant species we may mention *Equisetum arvense*, *Carex rigida*, *Deschampsia flexuosa*, *Agrostis canina*, *Festuca rubra*, *Rumex acetosa*, *Viola palustris*, *Taraxacum* and *Leontodon*.

Table 25 A, 5 shows the circling results for a smaller snow patch having a northern exposure. In its broad features this locality corresponds to the bottom vegetation of the large snow patches. Floristically there is the difference that *Vaccinium uliginosum* and *Empetrum nigrum* are present in the small snow patches, while *Sibbaldia procumbens* and *Gnaphalium supinum* are only present in the larger ones.

Just as, within the myri formations, the flói forms the extreme point in a sequence of changes conditioned by the length of the period when the ground is covered with water and the depth of the water-layer, so also, in the formations lying above the ground-water, the geiri shows a succession of changes conditioned by the length of time that the ground is covered with snow and the depth of the layer of snow. Passing from melar by way of the mo to geiri, the depth and duration of the snow-covering increases more and more. Melar is without snow or almost without snow throughout the winter, the mo has the snow-covering normal to the area, while the geiri is already covered at the first snowfall in the autumn, retains a deep and constant snow-covering throughout the winter, and only becomes bare again when the snow melts far on in the spring.

Now these conditions have the following effect on the vegetation. Where the snow-covering is slight, it consists principally of arctic species and life-forms, whereas, where it is deep, it consists of southern species and life-forms.

Thus melar has a Ch percentage of 52, an H percentage of 36, an A percentage of 81 and an A 3 percentage of 55. The E percentage is 0.

The mo (the knolly mo) has a Ch percentage of 38, an H percentage of 47, the A percentage is 71, the A 3 percentage 39, and the E 3 percentage 4.

The geiri (the *Geranium sylvaticum* belt) has a Ch percentage

of 31, the H percentage is 53, the A percentage 44, the A 3 percentage 24, and the E (3—2—1) percentage 35.

The Geranium belt represents the area where the characteristics peculiar to geiri are most striking. If we pass from the marginal zone through the Geranium belt to the bottom vegetation, or from a snow patch with a southern exposure to one with a northern exposure, the southern contingent is largest in the Geranium belt or the snow patch with the southern exposure, while it again decreases in the bottom vegetation or on the northern slope. This is especially due to a decrease in the southernmost E subgroups.

Looking for the cause of this change we find it in the unusually long period during which the formations in question are covered with snow. In the case of the southern types of plants, which obtain the most favourable life-conditions in the Geranium belt (that is to say, the greatest possible protection from the winter cold and the most favourable temperature in the period of vegetation), the long-lasting snow-covering causes the vegetation period to become too short for these plants.

The number and density of species which attain their highest values, 36 and 15 respectively, in the mo, have the values 32 and 13 in the Geranium belt. This diminution is continued in the bottom vegetation, so that here the number of species is only 21 and the density 10.

If these changes are continued, with the successive diminution of the number of species and the quantity of southern species, as a final result we may anticipate to find, at still greater altitudes above the sea, the *Salix herbacea* and *Sibbaldia* formations described by Helgi Jónsson and at still higher levels the *Anthelia*-vegetation.

At the level at which Arnarvatnsheiði is situated, in the lower zone of the mountain region, we have thus the following types of vegetation.

I. Melar, conditioned by a slight snow-covering and a comparatively strong desiccation of the soil.

II. The *Betula nana* mo, where the snow-covering is deeper and the moisture of the soil greater: while the melar vegetation is peculiar to the denudation area of solifluction, the *Betula nana* mo is peculiar to the accumulation area.

III. **The knolly mo.** The snow-covering and moisture of the soil are still greater. No solifluction, but incipient formation of knolls.

IV. **Jáðar**, peculiar to moderately moist soil with normal snow-covering and maximum formation of knolls.

V. **Mýri.** The soil is constantly moist, the ground-water coming up above the surface. Two formations may be distinguished, an upper, more dry, formation in which knolls occur, and a lower, more moist, formation in which the surface is level and without knolls.

VI. **Flói.** Constantly covered with water, the bottom level, no knoll formation.

VII. **Geiri.** Snow-covering deep, bottom comparatively moist, especially in the lower formations, surface level, no knolls.

The types of vegetation in other parts of the highlands seem to correspond to these.

VI. THE DISTRIBUTION OF SPECIES, SPECIES-GROUPS, AND LIFE-FORMS IN THE FORMATIONS, ARRANGED ACCORDING TO INCREASING PREVALENCE OF ONE AND THE SAME EXTERNAL FACTOR

In the two preceding chapters we have treated in more detail a series of Icelandic formations with respect to their environment and their floristic and biological characteristics. A very important part still remains to be treated, viz. a determination of the areas covered by the individual species within the tracts examined.

The most obvious method of determination would be to map the formations within the tracts examined, and determine their areas on the basis hereof. But this work would involve too much time and trouble if it were to be accomplished in a fairly reliable way.

A more practical method has been worked out by Thore Fries in 1919. The mode of procedure in this method, "the synecological line taxation method", is as follows. A system of definite lines, drawn according to more precise rules, is laid down, and the lengths of line covering the respective formations, are then measured. If the system of lines is correctly laid, that is to say, if the lines are laid sufficiently close together, the sum of the lengths of line covering a given formation will afford a measure for the area covered by the formation within the tract examined, and the proportion of the length of line covering a given formation to the total length of the line system will correspond to the proportion of the area covered by the formation to the total area of the tract examined. (Th. Fries, 1919, p. 8).

In my investigations of the Icelandic vegetation I did not employ Fries's line taxation method, a fact which I have often regretted during my elaboration of the material, but during investigations in Denmark I have often experienced how practical this method is compared with the usual mapping of the formations of an area. Thus I have the same experience of the line taxation method as has Thore Fries of Raunkiær's circling method

"the method, in my opinion, constitutes an ingenious and satisfactory solution of the problem." (Th. Fries, 1919, p. 4).

I can likewise fully support the author when he goes on to say, "Raunkiær's circling method and the synecological line taxation method complete each other. By the former we obtain exact knowledge of the nature of the units, by the latter of their area and distribution. Synecological plant geography should be able to make great progress in exactitude by these two methods. Synecology now need no more rank last in this respect among the various branches of botany, on the contrary, it should soon be able to take up its position as one of the first."

However, the results which these two methods will be able to produce, viz. an exact description of the plant series of the face of the earth, only constitute one aspect of plant geography, the geographical aspect. For such a description is primarily of importance in its bearing on geography. The botanical aspect proper will only appear when, in addition, we investigate the external factors which determine the distribution of the individual biological or systematic units.

If we follow the ordinary scientific method of investigating the facts in connection with a given unit by varying only one external factor at a time and as far as possible keeping all the other factors constant, this means, in the case of the doctrine of formations, that we must primarily examine the distribution of the individual species within the formations, arranged according to increasing prevalence of one and the same external factor. The resulting facts may then be made the basis of more detailed ecological considerations.

In the present chapter we have examined the distribution of a series of Icelandic species partly in relation to the Icelandic scale of moisture, partly in relation to the scale of snow-covering. The material employed is the same which was utilised for the formation statistics of the two preceding chapters. On the basis of this material we have further examined the distribution of Raunkiær's life-forms and the species groups in relation to the above-mentioned two scales.

The Scale of Moisture.

Under the treatment of the formations in the localities examined the degree of moisture has been more precisely described.

We may distinguish between an area in which the moisture of the soil is entirely dependent on the precipitation throughout the year, an area whose moisture throughout the year depends also on the ground-water, and an intermediate area in which the moisture of the soil depends on the precipitation in the summer, while in the winter it is also dependent on the ground-water. This area is represented by the jaðar vegetation.

If, on a gently sloping surface, we pass upwards from the jaðar vegetation, we may distinguish here between three different zones of moisture: a lower zone in the mo, where the influence of the ground-water is still demonstrable, the mo itself, where this influence no longer exists, and an upper zone (the mellar vegetation), which, on account of its open vegetation, is exposed to a stronger desiccation than the more densely covered mo.

If, from the jaðar vegetation, we pass downwards, we can likewise distinguish between three different zones of moisture: an upper myri formation, not very damp in the summer, a lower myri formation saturated with water, and finally the flói, which is covered with water throughout the year.

Thus we may distinguish between 7 different zones of moisture in Iceland.

- Zone I comprises the Elyna mo at Bjørk and the mellar vegetation on Lýngdalsheiði, at Lækjamót, and on Arnarvatnsheiði.
- Zone II comprises the Arctostaphylos mo at Bjørk, the ordinary mo at Lýngdalsheiði, the high mo at Lækjamót, the mo at Nordtunga, and the Betula nana mo on Arnarvatnsheiði.
- Zone III comprises the Calluna-Empetrum mo at Bjørk, the moist mo on Lýndalsheiði, and at Lækjamót, and the knolly mo on Arnarvatnsheiði.
- Zone IV comprises the jaðar vegetation at Bjørk, on Lýngdalsheiði, and on Arnarvatnsheiði.
- Zone V comprises the Salix myri at Bjørk and on Lýngdalsheiði, and the knolly myri on Arnarvatnsheiði.
- Zone VI comprises the Betula nana myri at Lækjamót and Bjørk and on Lýngdalsheiði, and the level myri on Arnarvatnsheiði.
- Zone VII, finally, comprises the flói vegetation at Bjørk, on Lýngdalsheiði at Lækjamót, and on Arnarvatnsheiði.

These 7 zones may be pointed out without difficulty wherever the ground does not slope too steeply. As soon as the ground becomes more rugged and uneven, irregularities in the distribution of the zones may be observed. One or more zones will not be developed; thus moist *mýri* may be observed to adjoin high mo without the intermediate zones having attained development. The interrelationship of the zones can, however, be confirmed wherever the mo, or the *mýri*, is the dominant feature of the landscape. In hollows in the mo the *jaðar* will always be the first type of vegetation to be met with, and with the progressive size and depth of the depression the other types will follow in the above-described sequence. Wherever an elevation occurs in the *mýri*, the types of vegetation will succeed each other from the edge of the *mýri* to the summit of the elevation in the same regular way in conformity to law. These conditions are repeated again and again in every part of the island.

Table 26 shows the distribution of the life-forms and the species-groups in relation to the scale of moisture in the various series of investigations. The Roman numerals I—VII correspond to the 7 zones of moisture mentioned above.

Life Forms. Their Distribution in Relation to the Scale of Moisture.

In a previous chapter (pp. 13—33) the influence of the climate on the prevalence of species-groups and life-forms in the flora was subjected to a more detailed investigation. As far as the life-forms were concerned Ch proved of special interest by the close correlation between the rise in the Ch percentage and the severity of the climate. Passing round the coast from South Iceland by way of western and northern Iceland to East Iceland, the Ch percentage showed a continuous rise, and passing from the level of the sea towards the snow-line, the same was the case, only in even greater degree. The same was the case with the A percentage.

The statistical investigations of the formations confirm this. Thus, if we compare the Ch percentage of the Elyna mo at Björk, the formation in the southern lowlands which is most arctic in character, with the melar at Lækjamót, the most pronounced arctic formation in the north country (both localities at a height of c. 100 m.), we shall see that in the former case the Ch percentage is 28, in

the latter 45. On Arnavatnsheiði, at a level of c. 500 m., the same formation shows a Ch percentage of 52.

Taking the mosathembur vegetation of Lýngdalsheiði from altitudes of c. 250 m., 332 m., and 400 m., we get the following scale for the Ch percentage: 10→55→68, with a corresponding rise of the A percentage: 75→90→100.

Thus the influence of the cold on the Ch and A species is beyond all doubt.

Table 26 shows the distribution of the life-forms in relation to the scale of moisture. A remarkable circumstance appears in connection with the chamaephytes. From a comparative minimum in zone IV (the jaðar vegetation) the Ch percentage increases in value, upwards as well as downwards. This applies equally to the Björk series, the Lýngdalsheiði series, and the highland series. In the Lækjamót series the increase does not appear in the lower part of the scale for the halla myri series, whereas the rule seems to apply to the fór myri series here.

It is difficult to find any plausible reason why Ch should thrive best in the mo and the myri, and badly in the intermediate jaðar. Anyhow, it is a fact that the environment in the jaðar is unfavourable to Ch. Species such as *Empetrum nigrum*, *Vaccinium uliginosum*, and *Betula nana* occur with a higher F.-percentage above as well as below the jaðar.

Possibly the cause may be found in the annual variations in the level of the water. It is of minor importance to Ch whether the moisture is great or small, if only it is the same all the time. If great variations take place, as is the case in jaðar where the plants grow now on damp, now on dry soil, Ch decline.

On the heaths of Jutland it may often be observed how great variations in the water level tend to kill the chamaephytes, and at the level of moisture corresponding to the jaðar, viz. the edge of the bog, the following facts may be observed. In the middle of the heath where the variations are only small, the chamaephytes play a prominent part in the composition of the vegetation, near the valley of the river where the variations are greater, the chamaephytes disappear. In a series of investigations on this zone of moisture at Nørholm Heath the former formation showed an average Ch percentage of 55, while the latter formation had only a Ch percentage of 4.

Possibly the depression of the Ch percentage in Zone IV may be referred to similar circumstances.

If we compare the A percentage and the Ch percentage in the scale of moisture, both series are seen to take a corresponding course with a relative minimum in Zone IV. Thus the depression may perhaps also be due to the temperature conditions which are more favourable to the vegetation in this zone than in those above and below.

The hemicryptophytes are peculiar to the upper, drier part of the scale of moisture with perhaps a slight indication of a rise from Zone I to Zone IV. From this zone onward there is, at any rate, a strong decrease. The maximum of the hemicryptophytes in the moderately moist area which coincides with the relative minimum of the chamaephytes is most pronounced in the highland tracts. The hemicryptophytes dominate more in the lowland than in the highland formations, and of the lowland formations those of the south country are more abundantly provided with H than those of the north country. Thus, in contrast to the chamaephytes, the hemicryptophytes seem to thrive best in a moderately moist environment of favourable temperature. This appears with even greater distinctness in the distribution of the species, as is sufficiently evident from the biological spectra in table 8 for the heath and mo vegetation, in contrast to the vegetation of the littoral meadows and the grassland.

The therophytes play no very great part in the composition of the vegetation in Iceland. They occur most abundantly in the relatively continental parts of Iceland, the highlands and the north country; in the rainy south country they hardly occur at all in the typical formations. In the north country they occur more abundantly in the lowlands than in the highlands.

In the scale of moisture Th attain two maxima, one in Zone I (melar), and one in Zone IV (jaðar). In the part showing the greatest moisture they do not occur at all. The rise in Zone IV is of special interest: for the individuals it is most marked in the highland series, for the species it is even more marked than for the individuals, as shown by the biological spectra of the vegetation of the littoral meadows and the grassland in Vestfirðir. The Th percentage for these two types of vegetation which correspond to the jaðar vegetation, is 15—16, for the heath and mo vegetation it is only 1—8.

As previously mentioned, the flag vegetation is peculiar to this level, and this type of vegetation has just those characteristics which were pointed out for Zone IV, or the jaðar vegetation, viz. a low chamaephyte percentage and high H and Th percentages; these conditions are, however, more pronounced in the flag than in the jaðar vegetation. Thus the forces which produce and sustain the flag vegetation act, though in slighter degree, wherever this level of moisture occurs, even where no flag is developed.

The cryptophytes, i. e. the helophytes and geophytes, are peculiar to the lower sections of the scale of moisture, just as Ch, Th, and H are peculiar to its upper sections. HH are most abundant in the lowlands and the south country, decreasing in quantity as we pass to higher levels. This agrees with the HH percentage in the Greenlandish local floras where, as previously shown, the HH percentage decreases from south to north along the west coast as well as the east coast.

As regards the distribution of HH in the scale of moisture, they naturally occur in the greatest quantity in the flói on soil that is constantly covered with water; thence they decrease strongly through the myri, until they disappear entirely in jaðar.

The geophytes have a similar distribution. In Zone VII, the dampest section of the scale, they attain their maximum; thence the G percentage decreases strongly and steadily throughout the scale until, in Zone I, they attain their minimum which is lowest in the north country and highland tracts, highest in the south country. Thus the geophytes, on this point too, present a contrast to the therophytes and chamaephytes.

In regard to species the cryptophytes show the same conformity to law; thus the freshwater vegetation of Vestfirðir has an HH percentage of 70, the myri vegetation an HH percentage of only 9. In the same locality the G percentage of the myri is 25, of the mo, 14, and of mellar only 9.

We have now seen the distribution of Raunkiær's life-forms in the Icelandic scale of moisture. From the circling results it appears that the individual life-forms attain their maximum development at different grades of the scale. Passing from the bottom to the top of the scale, the following sequence appears

Heloph. → Geoph. → Hemicryptoph. → Theroph. & Chamaeph.

In the 4 moisture series examined so far, the life-forms show, in the main, the same sequence.

If the biological spectra are based on species lists alone, we get the same sequence.

This distribution must be regarded as more specific to the life-forms than to conditions in Iceland.

In Denmark the vegetation of Nørholm Heath has been examined with the same minute graduation of the external factors as in Iceland. The sequence of the maxima of the life-forms in the scale of moisture was the same on Nørholm Heath (which, however, had more than 7 grades) as in Iceland, viz. HH, G, H, and Ch from below upwards. The rise in the Ch percentage in the lower section of the scale is not found here, however; on the other hand, there is a rise of the H percentage.

Raunkiær (1909, 1912), C. Olsen (1914, 1921), and Grøntved (1927) examined the vegetation on solid soil exposed to the sun. From their researches it will likewise appear that, if biological spectra for the various (more diffusely limited) zones of moisture are worked out on the basis of the circling results, the sequence will be HH, G, H, Ch, and Th.

If biological spectra for the various zones of moisture from sunny open solid soil were worked out on the basis of the species lists alone, the sequence of life-forms was still seen to be the same.

The correlation between moisture of soil and life-form pointed out above must be said, therefore, to be generally valid. In considering the physical causes active in the formation of life-forms, a knowledge of this correlation is indispensable.

The Species-Groups. Their Distribution in the Scale of Moisture.

On the basis of particulars of the presence and quantitative distribution of the individual species in northern Europe and the adjacent arctic regions we have, in a previous chapter, divided the Icelandic flora into groups according to the temperature requirements of the species.

The flora was first divided into two large groups: the A group which has its main distribution in arctic regions to the north of or, in mountain regions, above, the tree limit, the 20 per cent Ch biocline; and the E group which has its main distribution in the

TABLE 26. **The Distribution of Species
Groups and Life Forms in the Scale of Moisture.**

1. The Björk Series. 2. The Lýngdalsheiði Series. 3. The Lækjamót Series. 4. The Arnarvatnshéiði Series. (Cfr. the text).

	Pointsum	Number of species	Density of species	A	E	A3	A2	A1	E4	E3	E2	E1	Ph	Ch	H	G	HH	Th
1. I.....	4536	29	11.4	52	48	30	11	11	30	11	4	2	»	28	56	16	»	»
II.....	4096	30	13.6	33	67	18	9	6	33	13	21	0.3	»	39	47	14	»	0.2
III.....	4436	40	14.8	39	61	19	10	10	33	11	17	0.5	»	29	52	18	»	0.1
IV.....	2756	42	13.8	36	64	15	8	13	36	14	15	0.3	»	22	54	23	2	0.2
V.....	2768	39	13.9	37	63	14	11	11	43	18	3	»	»	25	34	33	8	»
VI.....	1920	26	9.6	41	59	10	17	13	41	15	3	»	»	33	9	45	13	»
VII.....	376	5	1.9	24	76	»	3	22	9	67	»	»	»	»	63	37	»	»
2. I.....	3852	18	5.5	60	40	36	19	5	30	10	0.5	0.2	»	43	39	18	»	»
II.....	3644	34	13.3	50	50	29	10	11	25	14	10	1	»	26	56	17	»	0.3
III.....	1384	32	13.8	51	49	23	13	15	24	15	11	»	»	23	59	18	»	»
IV.....	1376	38	13.8	43	57	20	12	11	30	15	12	»	»	12	53	34	1	0.3
V.....	1076	34	10.8	47	52	21	17	9	33	16	4	»	»	19	34	41	6	0.4
VI.....	2832	21	9.4	51	49	17	22	18	34	15	»	»	»	29	13	52	6	»
VII.....	228	2	1.1	2	98	»	»	2	36	63	»	»	»	»	36	65	»	»
3. 1.....	2058	27	6.9	75	25	52	16	7	24	1	1	0.2	»	45	47	5	»	3
2.....	3480	39	17.4	64	36	39	18	7	25	7	4	0.1	»	35	49	14	»	2
3.....	3168	43	15.9	57	43	33	16	8	23	10	8	2	»	25	58	14	»	3
4.....	2228	33	11.2	50	50	23	25	2	24	17	9	»	»	13	40	46	»	2
5.....	780	29	7.8	51	49	17	24	10	24	17	8	»	»	11	19	62	8	1
6.....	1172	14	5.9	30	70	22	17	2	26	30	15	»	»	0.3	25	65	9	»
5'.....	908	27	9.1	44	56	19	23	1	44	13	»	»	»	23	22	55	»	»
6'.....	204	3	2.0	51	49	2	»	49	49	»	»	»	»	»	»	100	»	»
4. I.....	4748	27	7.9	81	19	55	20	6	19	»	»	»	»	52	36	10	»	2
II.....	5664	32	11.3	70	30	43	24	3	29	1	»	»	»	48	37	15	»	1
III.....	7184	35	14.4	71	29	39	25	7	24	4	»	»	»	38	47	15	»	0.3
IV.....	6008	38	12.0	63	37	34	22	7	28	6	3	»	»	21	51	27	»	2
V.....	3392	23	8.5	56	44	43	12	2	43	1	»	»	»	28	26	46	1	1
VI.....	2344	11	4.7	66	34	33	22	12	29	4	»	»	»	14	11	71	4	»
VII.....	932	7	2.4	35	65	20	10	5	53	13	»	»	»	6	15	75	4	»
Average I .	13.136	25	8.3	64	36	40	17	7	26	7	2	1	»	41	44	15	»	0.7
II..	16.404	32	12.7	51	49	30	14	7	29	9	10	0.4	»	38	47	15	»	0.5
III..	13.004	36	14.3	54	46	27	16	11	27	10	9	0.2	»	30	53	17	»	0.1
IV..	10.140	39	13.2	47	53	23	14	10	31	12	10	0.1	»	18	53	28	1	1
V..	7.136	32	11.1	47	53	26	13	7	40	12	2	»	»	24	31	40	5	0.5
VI..	7.096	19	7.9	53	47	20	20	13	35	12	1	»	»	25	11	56	8	»
VII..	1.536	5	1.8	20	80	7	4	10	33	48	»	»	»	2	17	68	14	»

temperate zones, to the south of, or below, the 20 per cent Ch biochore.

The A group was again divided into 3 minor groups according to the temperature requirements of the groups.

The A 1 group requires the highest temperature and is only found in subarctic regions. 66° N. lat. in West Greenland was chosen as a practical northern limit.

The A 2 group does not require so high a temperature, yet it does not occur in the most pronouncedly arctic regions. The northern limit of the group in West Greenland lies south of 76° N. lat.

The A 3 group is of common occurrence as far north as northern Greenland, hence it is the group that thrives best in the most extreme cold.

While cold, i. e. a low temperature, together with a varying amount of heat is indispensable for the A groups, heat is indispensable to the E group. In the latter group we may likewise distinguish a series of types according to their temperature requirements. Hence group E was divided into 4 minor groups of which E 1 required most heat, E 4 least.

The species of the E 1 group have their northern limit in Scandinavia that is to say, they belong to southern Scandinavia.

The E 2 group has no northern limit in Scandinavia, but does not occur in Greenland.

The E 3 group is composed of Icelandic species which occur in Greenland, but south of 66° N. lat.

The E 4 group occurs in Greenland north of this line.

The distribution of the species groups in the various parts of Iceland as well as in the Icelandic altitudinal zones fully confirms the above described distribution of the groups, both as regards quantity and as regards mere presence. Thus the A group occurs most abundantly and with the greatest number of species in the north and in the highland tracts, whereas the E group is the dominant group in the lowlands and the south country.

Of the A sub-groups A 1 prefers the lowland, A 2 the lower tracts of the highland, and A 3 the upper tracts of the highland.

Of the E sub-groups E 4 is of common occurrence everywhere, though there is an appreciable decrease in the upper tracts of the highlands. E 3 occurs most frequently in the lowlands. E 2 and especially E 1 occurs solely, and only in scattered specimens, in the

lowlands. These plants find the most favourable conditions of growth round the hot springs.

The circling investigations closely confirm these results. The A percentage of the formations is higher in the highland than in lowland tracts, and higher in North Iceland than in South Iceland. The same applies to the sub-groups, A 1 showing a steady decrease in quantity from the lowlands to the highlands: at Björk and Lækjamót the average A 1 percentages are 12.1, at Lýngdalur the A 1 percentage is 9.1, and at Arnarvatnshéiði it is 5.8.

A 2 occurs more frequently in the highlands than in the lowlands, and more frequently in North Iceland than in South Iceland, this is the case too with A 3, only in an even more marked degree.

The E sub-groups show similar relations. E 4 occurs with equal frequency in the highland and lowland tracts. E 3 occurs most frequently in the lowlands, especially in the south country. The same applies in even greater degree to E 2 and especially to E 1.

Table 26 shows the numerical values and their variations according to altitude and district.

Table 26 shows the distribution of the species groups in the scale of moisture.

The A group shows the same depression on moderately moist soil as the chamaephytes; from Zone IV the A percentage shows an increase, both upwards in the mo and downwards in the myri. In Zone VII, the flói, the A percentage reaches its lowest value.

The individual sub-groups show different relations; while the A 3 group decreases steadily as we pass downwards in the scale from mo through jaðar to myri, the reverse is the case with the two other groups, so that the increase of A in the lower section must be ascribed to A 2 and A 1. These relations are most plainly illustrated in the lowland series: Björk, Lýngdalur, and Lækjamót.

The individual sub-groups of E play a very different part in the composition of the vegetation. E 4 occurs in the greatest quantity, then successively E 3, E 2, and E 1.

While E 4 and especially E 3 must be said to prefer the damper section of the scale, the reverse is the case with E 2 and E 1 which only occur in the mo formations. In the Lækjamót series, however, E 2 forms an exception to this rule, for, similarly to E 4 and E 3, this group increases with increasing moisture of the soil.

Even if the 7 sub-groups cannot perhaps be said to form a continuous scale of adaptation to decreasing temperature, this is at

any rate the case within the sub-groups of each of the two larger groups, and this justifies a linear grouping like the one employed. If now we regard the spectra of the scale of moisture as a whole, as a series-spectrum, it shows a pronounced tendency to form a wedge downwards, produced by a decrease in quantity of the sub-groups of both main groups from without inwards. This wedge shape appears in all the series.

The wedge shape of the series-spectrum must be put down to the different temperature conditions in the different sections of the scale.

Thus the variations in temperature in the upper part of the scale will be greater than in the lower part since the specific heat of the water will act as a buffer here against changes of temperature. To this must be added the fact that considerably more water will evaporate from the damper than from the drier areas, and since the temperature at which water evaporates, as well as its specific heat, is very high, this will in practice mean a slower and slighter heating of a moist than of a dry area. In the summer, therefore, the temperature will be lower in the former than in the latter area. In the winter the reverse will be the case. If, in addition, the temperature drops below zero, considerable amounts of heat will be liberated within the moist areas, viz. the heat which has become latent by the thawing of the ice, the effect of which will be that a damp soil will freeze slower and not to such depths as a dry soil.

In the case of moderately moist soil, one more circumstance must be noted. This zone is relatively dry in the summer, and relatively moist in the winter, which gives it more or less the advantages of dry soil in the summer and of wet soil in the winter. All in all this area will have more favourable temperature conditions than the areas above and below.

The interaction of temperature conditions and vegetation in the various zones of moisture will thus be as follows: —

A. Melar (Zone I) is in pronounced degree cold in the winter as well as warm in the summer. Hence plants which require much cold (Ch and A 3 species) and much heat (E 2+1 species) thrive well here. In contrast to the other zones of moisture it is, however, bare of snow in the winter. This will further encourage the A 3 species, while the E 2+1 species will decrease in quantity.

B. The Mo (Zones II—III) is likewise cold in winter and warm

in summer, though in less degree than Zone I. Hence the same types of plants occur here.

C. *Jaðar* (Zone IV). As previously indicated, this zone must be regarded as relatively warm in winter and warm in summer, owing to the variations in the level of ground-water. Hence the result is that the vegetation consists in marked degree of southern types, H, Th, and E species.

D. *Mýri* (Zones V—VI) is warm in the winter but cold in the summer. Hence southern plants requiring much heat (E 2+1 species) and northern plants requiring much cold (A 3 species) thrive badly or are unable to thrive here. As a matter of fact the vegetation consists of southern plants requiring little heat (E 4+3 species) and northern plants requiring little cold (A 2+1 species).

E. *Flói* (Zone VII). Here the vegetation is covered by so deep a layer of water that the frost hardly reaches it in the winter. Hence it is never exposed to the conditions required by arctic plants; consequently these are absent at any rate in the lowlands and as compared with the *mýri* formations. In the summer, too, the vegetation is covered by water. The heat which benefits the plants on drier soils is latent in the water here. The result is a relatively low temperature which excludes the southern plants requiring more heat. Hence the species group spectrum is compressed to the central parts of the spectrum.

Between *halla mýri* and *fór mýri* there is a peculiar difference in regard to the species group spectrum.

As previously mentioned, the difference between the *halla mýri* and the *fór mýri* is this, that *halla mýri* appears where the ground water comes to the surface, while the *fór mýri* is dependent for its moisture on the surface precipitation water. While the temperature of the water is to a certain extent dependent on the temperature of the air in the latter case, the temperature of the water in the *halla mýri* is dependent on that of the ground-water, which again is equal to the annual mean temperature of the locality in question. In the winter there will be a constantly varying amount of relatively warm water in the *halla mýri* to be cooled, whereas, in the *fór mýri*, there will be a constant amount of water to be cooled, and the result must be that the temperature of the *halla mýri* in the winter must be higher than that of the *fór mýri*. In the summer the reverse must be the case. The heat in the *halla mýri* will have a constantly varying amount of

now relatively cold water to heat, while in the fór myri there will be a constant amount of water to be heated, and the result will be that in the summer the temperature of the fór myri will be higher than that of the halla myri. Which will be best for the vegetation must depend on the relative lengths of summer and winter. Where summer is the longer season, the result will be a relative cooling of the locality in question and a stronger cooling than that which is conditioned by stagnant water. Where winter is the longer season, the locality in question will offer favourable temperature conditions for the vegetation, even though the summer, short as it is, must also exert its influence.

The former conditions prevail in Denmark, the latter in Iceland. For Denmark A. Mentz (1912) has shown that the Paludella bog is tenanted by a series of northern-alpine species not found elsewhere in this country. Thus the Paludella bog offers more favourable growth conditions to arctic plants than other types of bogs. The same is the case in Iceland. In the halla myri at Lækjamót the quantity of A 2 species is considerably higher than in the corresponding fór myri zones in the south country, while the quantity of A 2 + A 1 species is higher in the halla myri of the valley slopes than in the fór myri of the valley bottom.

Hence the cold water peculiar to the halla myri in the summer has even in Iceland a noticeable influence on the vegetation and gives it an arctic character.

The effect on the vegetation of the warm water in winter is, however, much stronger.

If, in a fór myri series, we pass from the drier to the more moist zones, the E 3 percentage has practically the same value throughout the zones until we reach the very wettest, when it shows a very great rise. In the halla myri series the E 3 percentage has its lowest value in the drier zones, whence it rises steadily until it attains its highest value in the dampest zone.

In the fór myri series E 2 attains its highest value in the driest to moderately moist zones (mo and jaðar), whereas, in the dampest zones (myri and flói), it has decreased much or is entirely absent. In the halla myri, on the other hand, the E 2 percentage rises on the passage from dry to moist soil; where there is the highest degree of moisture, the E 2 percentage is highest.

This difference between the halla myri and the fór myri is most naturally explained if we assume that it is

	Average							Björk c. 100 m. o. H.							Lyngdalur							Arnarvatnshœði													
	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII							
<i>Tostostaphylos uva ursi</i> ...	0.3	31	1	2	»	»	»	1	93	3	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»								
<i>Luna vulgaris</i> ...	1.3	29	28	2	»	»	»	4	85	6	»	»	29	58	16	»	»	»	»	»	»	»	»	»	»	»	»								
<i>Rumus serpyllum</i> ...	53	50	32	4	»	»	»	95	96	91	40	32	»	46	89	100	72	28	1	»	49	8	11	1	2	»	»								
<i>Ostis canina</i> ...	47	64	77	39	20	0.3	»	40	17	43	34	12	4	2	66	80	20	4	3	»	18	66	5	»	»	»	»								
<i>Ginnella selaginoides</i> ...	14	34	63	20	5	2	»	26	60	48	44	12	6	»	3	73	80	40	16	»	»	»	»	»	»	»	»								
<i>Rigin boreale</i> ...	10	44	43	28	9	2	»	20	4	8	4	»	»	1	10	»	»	»	»	»	»	6	10	»	»	»	»								
— <i>verum</i> ...	7	5	3	1	»	»	»	18	53	37	8	»	»	6	64	60	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia flexuosa</i> ...	8	39	34	6	2	»	»	11	12	4	»	»	»	14	8	»	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia xanthoxanthum odoratum</i> ...	4	9	4	1	»	»	»	5	15	9	10	6	»	2	16	16	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia multiflora</i> ...	1.7	6	8	10	2	»	»	18	35	60	18	»	»	50	28	8	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia pratense</i> ...	6	28	29	11	3	»	»	1	3	21	4	»	»	1	12	»	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia officinale</i> ...	0.3	1.3	9	18	1.3	»	»	19	58	6	»	»	1	28	64	4	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia caespitosa</i> ...	0.3	16	41	3	»	»	»	1	19	70	4	»	»	5	»	»	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia tenuis</i> ...	2	6	23	1.3	»	»	»	7	20	18	»	»	1	12	12	»	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia sparsiflora</i> ...	3	11	10	»	»	»	»	2	5	24	52	68	2	»	8	»	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia lanata</i> ...	2	»	»	»	»	»	»	7	48	76	6	»	3	20	36	44	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia palustris</i> ...	1	9	31	40	2	»	»	16	74	42	2	»	»	12	56	15	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia palustre</i> ...	2	9	44	19	1	»	»	54	100	100	66	»	»	88	100	97	68	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia Goodenoughii</i> ...	0.3	47	67	66	53	»	»	6	42	96	50	»	»	4	100	95	2	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia chordorrhiza</i> ...	2	3.3	49	80	20	»	»	4	20	36	50	»	»	»	4	44	»	»	»	»	»	»	»	»	»	»	»								
— <i>rostrata</i> ...	2	1.3	9	34	20	»	»	3	11	1	»	»	10	28	2	»	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia trifoliata</i> ...	2	»	»	»	»	»	»	45	40	48	6	»	»	36	56	4	»	»	»	»	»	»	»	»	»	»	»								
<i>Acicus trifidus</i> ...	41	45	51	6	1	»	»	37	37	19	12	»	»	26	50	48	»	»	»	»	»	»	»	»	»	»	»								
<i>Uchampsia villosa</i> ...	44	44	43	14	3	1	»	88	53	53	42	8	»	13	77	76	24	12	»	»	4	18	37	36	1	»	»								
<i>Uchampsia Normanni</i> ...	35	49	55	34	7	»	»	53	12	45	4	»	»	3	22	»	»	»	»	»	»	6	32	45	6	1	»	»							
<i>Uchampsia Bellardi</i> ...	21	22	30	3	1	»	»	22	7	11	2	»	»	3	35	28	12	4	»	»	»	»	7	11	27	1	1	»	»						
<i>Uchampsia spicatum</i> ...	11	18	22	5	2	1	»	39	43	65	20	62	»	6	26	64	90	48	»	»	»	»	5	76	88	86	23	»	»						
<i>Uchampsia alcticrum alpinum</i> ...	15	48	69	87	55	22	»	97	95	99	98	84	14	»	45	93	92	92	25	»	»	»	»	11	77	88	66	5	»	»					
<i>Uchampsia stictica rubra</i> ...	51	88	93	87	60	13	»	38	77	73	74	72	10	»	42	36	60	72	44	»	»	»	»	»	»	»	»	»	»	»					
— <i>ovina</i> ...	46	52	56	42	5	5	»	90	100	100	72	86	»	45	74	64	20	48	16	»	»	»	»	»	»	»	»	»	»	»					
<i>Uchampsia nigrum</i> ...	52	94	97	42	52	49	»	1	51	65	51	11	»	8	2	86	100	60	60	33	»	»	»	»	»	»	»	»	»	»					
<i>Uchampsia lichenoides</i> ...	52	73	58	38	5	1	»	85	71	77	42	6	»	62	86	96	92	93	»	78	98	96	98	86	11	»	»	»	»	»					
<i>Uchampsia herbacea</i> ...	29	68	81	80	41	1	»	4	65	76	92	94	80	»	2	8	»	7	»	3	4	9	1	»	»	»	»	»	»	»					
<i>Uchampsia rigida</i> ...	68	87	95	93	95	66	»	3	5	»	4	8	»	8	14	12	4	24	92	»	4	76	72	7	39	7	»	»	»	»	»				
<i>Uchampsia viviparum</i> ...	2	5	5	0.3	1.3	3	»	8	80	49	66	78	94	»	1	15	12	40	8	»	»	»	»	»	»	»	»	»	»	»	»				
<i>Unguiculula vulgaris</i> ...	7	57	44	26	47	64	»	2	1	»	»	»	»	2	1	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»				
<i>Unguiculula uliginosum</i> ...	8	15	1	1	8	53	»	20	19	19	28	»	1	16	40	38	»	4	12	48	16	»	»	»	»	»	»	»	»	»	»				
<i>Unguiculula nana</i> ...	8	17	36	32	26	4	»	10	10	16	40	38	»	26	48	48	48	24	4	»	»	»	»	»	»	»	»	»	»	»	»				
<i>Unguiculula variegatum</i> ...	4	10	22	55	34	1	»	1	8	64	70	40	12	»	18	86	90	12	»	»	»	»	»	»	»	»	»	»	»	»	»	»			
— <i>arvense</i> ...	4	11	41	59	38	10	1	13	8	64	70	40	12	»	1	2	70	54	6	»	»	»	»	»	»	»	»	»	»	»	»	»			
<i>Unguiculula pratensis</i> ...	4	27	78	81	37	»	»	13	7	»	»	»	»	18	14	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»		
<i>Unguiculula polystachyum</i> ...	2	1	10	53	48	10	»	20	7	9	»	»	15	26	24	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»		
<i>Unguiculula rariflora</i> ...	25	8	5	9	»	»	»	1	»	»	»	»	2	1	3	17	4	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	
<i>Verasterium alpinum</i> ...	21	9	9	»	»	»	»	20	7	9	»	»	16	2	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	
<i>Dryas octopetala</i> ...	18	8	5	3	»	»	»	1	»	»	»	»	2	1	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»
<i>Poa glauca</i> ...	33	32	28	6	»	»	»	0.3	»	1	»	»	1	»	24	4	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»
<i>Silene aculea</i> ...	8	8	7	5	0.3	»	»	0.3	»	0.7	»	»	1	»	12	4	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»
<i>Armeria vulgaris</i> ...	1.2	3	11	1.7	0.3	»	»	0.7	»	1	»	»	1	»	11	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»	»
<i>Bartschia alpina</i> ...	1.3	4	6	0.7	»	»	»	»	1	»	»	»	»	2	1	»																			

the result of the effect on the halla myri of the warm water in the winter.

The Distribution of the Species in the Scale of Moisture.

Table 27 shows the distribution of the species in the scale of moisture respectively at Bjørk, on Lýngdalsheiði, and on Arnarvatnshéiði. A special column further shows the average values for these three localities.

The Lækjamót series has not been included in the table since the myri formations here differ in several respects from the above mentioned, thus causing some deviations which are not due to the conditions of moisture. On the whole, however, the distribution of the species in the scale of moisture in the Lækjamot series confirms the relations stated below.

In order to facilitate a general view the species have been grouped according as they occur with the greater frequency in the lowland formations or in the highland formations, or with equal frequency in both. Within each of these groups the species have then been arranged with the least »moisture-loving« first and the most »moisture-loving« last. Considerations of space have, however, necessitated the exclusion of some more rarely occurring species.

The figure marked against a given species in a column is the average F.-percentage of the species in question for the zone of moisture of the locality in question. Thus in the Elyna mo at Bjørk, *Festuca rubra* has the frequency percentages 96, 96, 100, and 96 in the 4 localities there examined. The sum, 388, divided by the number of the localities, 4, makes 97, which is the figure marked against *Festuca rubra* in table 27, Bjørk I.

If, next, we consider the distribution of the species in the scale of moisture, it is an extremely variegated picture that meets the eye both as regards quantitative distribution, that is to say, the average distance of the individuals, and as regards the mode of distribution in the scale. Some species show a low F.-percentage (i. e. a great average distance between the individuals), others a high F.-percentage (i. e. a small average distance between the individuals). Some species occur only in a small number of moisture classes, others in a larger number or in all classes. Some species only occur in the dry classes, others only in the moderately moist, others again only in the moist etc. But to whichever class or classes a

species belongs, it applies to all species that there is one class of moisture in which the species attains its highest F.-percentage and shortest distance between the individuals, and outside which the F.-percentage decreases and the distance between the individuals increases whether we go up or down the scale of moisture.

The distribution of the species in the scale may afford ground for the setting up of a series of types characterised by the magnitude of the F.-percentage, the position of the maximum in the scale, the number of classes in which the species occurs etc. etc., and in time it will be necessary to introduce a terminology in order to characterise briefly the relations of a species within an area. At the present time, while such investigations are still in their inception, there is no reason to set up such a system, especially since a good deal of material would be requisite for such a purpose. This part of the investigation must therefore be left until a later period. In this connection it will suffice, as was the main object of our investigation, to establish the fact that a species is closely identified with a definite degree of moisture of the soil. If there is any change in the degree of moisture, no matter in what direction, the F.-percentage of the species will change simultaneously, and the greater the change in the degree of moisture, the greater, too, will be the change in the F.-percentage, until such conditions of moisture are reached as entirely exclude the species. The species reacts identically to changes in moisture wherever it occurs.

The table shows how markedly this is the case in the three localities Björk, Lýngdalur, and Arnarvatnsheiði therein indicated. These three localities have been selected at random from the areas of distribution of the species discussed, and there is no reason to suppose that an investigation in other localities under the same external conditions would give a picture of the relation of the species concerned to the degree of moisture essentially different from that shown in the table. Greater certainty might of course be gained by an increased number of investigations, in that the influence on the magnitude of the F.-percentage of accidental factors, i. e. factors not determined by the degree of moisture, would be precluded or diminished.

The distribution of a species in a scale of external factors is just as constant and »good« a character in a species as any morphological or anatomical character.

TABLE 28.

A, B, C and D denote the different series of types of moisture (cf. text).

	I	II	III	IV	V	VI	VII
A. <i>Minuartia verna</i>	16	»	»	»	»	»	»
<i>Thymus serpyllum</i>	53	50	32	4	»	»	»
<i>Juncus trifidus</i>	41	45	51	6	1	»	»
<i>Selaginella selaginoides</i>	14	34	63	20	5	2	»
<i>Cardamine pratensis</i>	4	11	41	59	38	10	1
<i>Viola palustris</i>	»	1	9	31	40	2	»
<i>Carex Goodenoughii</i>	»	»	1	47	67	66	53
* <i>Eriophorum polystachyum</i> ...	»	»	»	14	79	81	100
* <i>Carex rostrata</i>	»	»	»	4	20	36	50
B. <i>Poa alpina</i>	3	3	10	12	2	1	»
<i>Equisetum variegatum</i>	8	17	36	32	26	4	4
<i>Polygonum viviparum</i>	68	87	95	93	95	86	4
C. <i>Cardamine pratensis</i>	4	11	41	59	38	10	1
<i>Deschampsia cæspitosa</i>	»	1	16	41	3	»	»
* <i>Carex capitata</i>	»	»	»	8	»	»	»
D. <i>Empetrum nigrum</i>	»	94	97	42	52	49	»
<i>Vaccinium uliginosum</i>	»	57	44	26	47	64	»
<i>Betula nana</i>	»	15	1	1	8	53	»

In considering the ecology of a species, a knowledge of both groups of characters is equally necessary.

Table 28 shows a selection of types of moisture differing in respect of position and magnitude of the maximum and the number of classes over which the species is distributed. A number of deviating species are given at last.

A. The individual species in the series *Minuartia verna*, *Thymus serpyllum* . . . (the A series) are characterised by a pronounced maximum differently situated for the different species and at different levels. From the maximum class the F-percentage decreases equally in both directions or from the edge of the scale towards its middle.

B. *Poa alpina*, *Equisetum variegatum*, and *Polygonum viviparum* differ from the above species in that they are equally distributed over all classes of moisture; they differ from each other by the F percentage which is low for *Poa alpina*, somewhat higher for

Equisetum variegatum and very high for *Polygonum viviparum*, corresponding to a dense growth of *Polygonum viviparum*, a somewhat more scattered growth of *Equisetum variegatum*, and a very scattered growth of *Poa alpina*.

C. A third series is represented by *Cardamine pratensis*, *Deschampsia caespitosa*, and *Carex capitata*. These species all have their maximum frequency percentage in class IV; they differ from each other in the magnitude of the F-percentage. For *Cardamine pratensis* the F percentage is 59, for *Deschampsia caespitosa* it is 41, and for *Carex capitata* 8. They also differ in the number of classes over which they are distributed: *Cardamine pratensis* occurs in all classes of moisture, I—VII, *Deschampsia caespitosa* in classes II—V, and *Carex capitata* only in class IV.

D. Most Icelandic species show the above-mentioned regular distribution in the scale of moisture. A small number of species deviate in that they have two maxima with an intermediate relative minimum. These species are represented by *Empetrum nigrum*, *Vaccinium uliginosum*, and *Betula nana*. In a previous section on the distribution of the chamaephytes in the scale of moisture we attempted to explain these facts. The relative minimum is due to annual variations in the water level.

Scale of Snow-Covering. Distribution of Species, Species-Groups, and Life-Forms in the Same.

For the present it is not possible to set up a scale of snow-covering as minutely graduated as the scale of moisture. The reason is that so far the depth and duration of the snow-covering have not been investigated. In the individual localities it is easy enough to observe the effect on the vegetation of the different depths of the snow-covering, but comparisons between the various localities are rendered difficult by the fact that we have no exact particulars on which to base a comparison between the scales of snow-covering of the different localities. According to Thoroddsen (1914) the snow lies longer and is of greater depth in the north country than in the south-west, and in the south country there may be no snow at all during a long period. In the highland tracts the depth and duration of the snow-covering is greater than in the lowlands. These facts must be taken into consideration in a comparison between the differences in vegetation at the various stations.

Under the treatment of the formations in the various localities examined, the causes of the differences in vegetation have been more precisely stated. At Bjørk in the south country the difference between the Elyna mo and the Arctostaphylos mo was caused, amongst other things, by a difference in the depth of the snow-covering. The Elyna mo has a relatively thin covering of snow, that of the Arctostaphylos mo is somewhat deeper. However, the difference is not considerable enough to cause the appearance of two different types of vegetation. At Nordtunga in the south-west country mo and forest-ground are covered by snow of different depths; while the mo has the snow-covering normally occurring in that part of the country, the forest-ground is covered by a considerable layer of snow throughout the winter. At Lækjamót in the north country, the mo has likewise the normal snow-covering, whereas the melar is bare of snow. All these localities are lowland localities situated at c. 50—100 m above sea-level. If we pass from the lowlands to the highlands, the difference in the scale of snow-covering will become increasingly evident. At Lýngdalur in the south country (c. 250 m above sea-level), three types of vegetation are easily distinguished. The difference between these three types, mosathembur* and melar with little or no snow-covering, mo with a normal snow-covering, and geiri with a deep and constant snow-covering, is due to the difference in the snow-covering. In some places a transitional form between mo and mosathembur had developed, with an intermediate depth of snow.

At Thrasaborgir (c. 400 m above sea-level) the three types mosathembur, mo and geiri were likewise developed.

On Arnarvatnsheiði near Úlfsvatn at an altitude of c. 500 m above sea-level, the scale of snow-covering was further differentiated. The 5 types of vegetation, melar, *Betula-nana* mo, the knolly mo, the sides of the snow patches, and the bottoms and north sides of the snow patches, represent 5 different degrees of snow-covering, where the first type has the slightest snow-covering of the shortest duration, the last, the deepest snow-covering of the longest duration,

Table 29 gives the distribution of the species in the scales of snow-covering of the 6 localities mentioned above. Within each locality the formation most devoid of snow is given first, furthest to the left, while the formation with the deepest snow-covering is put last, furthest to the right. Bjørk a is the Elyna mo, Bjørk b

the *Arctostaphylos* mo. Lýngdalur a, b, c, d, and e are respectively mosathembur, melar, transitional forms between mosathembur and mo, mo and geiri. Thrasaborgir a, b, and c are respectively mosathembur, mo and geiri. Lækjamót a and b are melar and the high mo. Norðtunga a, b, and c are the mo, the vegetation in the forest glades, and the vegetation on the forest-ground. Arnarvatnsheiði a, b, c, d, and e are respectively melar, *Betula-nana* mo, the knolly mo, the vegetation on the sides of the snow patches, and the vegetation on the bottom of the snow patches with a northern exposure.

A comparison of the mean values has been attempted and is likewise given in the table. The scale is divided into three divisions. I represents the types of vegetation bare of snow, melar (I b), and mosathembur (I a). II represents types with normal snow-covering, viz. the mo. III represents types of vegetation with a constant snow-covering, i. e. geiri and forest. In the calculation of the mean values the deviating localities have been omitted, viz. Björk a and b, Lýngdalur c, and Norðtunga c. The figures under I a are thus the mean values of Lýngdalur a and Thrasaborgir a; I b the mean values of Lýngdalur b, Lækjamót a, and Arnarvatnsheiði a. II represents Lýngdalur d, Thrasaborgir b, Lækjamót b, Norðtunga a, and Arnarvatnsheiði b and c. III, finally, represents the mean values of Lýngdalur e, Thrasaborgir c, Norðtunga b, and Arnarvatnsheiði d and e.

The distribution of species in the scale of snow-covering is as the distribution of species in the scale of moisture. Some species attain their maximum F.-percentage in class I, others in class II, others again in class III. Some species have a high frequency percentage in one of the classes, others in two classes, either I and II or II and III; only a small number of species occur with a high frequency percentage in all classes.

A comparison between the different scales of snow-covering shows in what uniform proportions the species occur in the different localities. It may be laid down as a main rule that the species react uniformly to the same changes in respect of snow-covering. A species which, in one locality, attains its maximum F.-percentage where there is a normal snow-covering but decreases if the snow-covering changes no matter in what way, will behave in the same way in all the other localities.

TABLE 29.

The Distribution of the Species in the

	Average			Bjørk		Lyngdalur			
	I b (I a)	II	III	a	b	a	b	c	d
Saxifraga caespitosa	4	»	»	»	»	»	»	»	»
Arenaria ciliata	5	»	»	»	»	»	»	»	»
Luzula arcuata	6	+	»	»	»	»	5	»	»
Saxifraga oppositifolia	14	»	»	»	»	»	»	»	»
Arabis petreæ	18	»	»	»	»	»	11	»	»
Minuartia verna	19	2	»	»	»	»	»	»	»
Poa glauca	30	10	+	7	»	»	3	20	17
Dryas octopetala	31	23	»	»	»	»	21	»	»
Cerastium alpinum	37 (3)	11	»	18	»	5	18	32	14
Silene acaulis	45 (6)	43	+	20	7	3	15	12	26
Luzula spicata	47 (2)	47	1	37	37	2	26	60	50
Thymus serpyllum	44	42	6	80	84	»	29	8	58
Festuca ovina	48 (2)	32	9	38	77	1	42	32	36
Carex rigida	1 (66)	69	73	85	71	92	2	84	86
Salix herbacea	37 (55)	79	66	51	60	14	45	68	74
Polygonum viviparum	58 (23)	90	53	65	76	14	62	56	86
Empetrum nigrum	22 (5)	86	73	90	100	2	38	64	88
Festuca rubra	26 (27)	89	65	97	95	48	45	84	93
Thalictrum alpinum	10 (25)	71	38	39	43	41	»	40	26
Galium Normannii	14 (3)	51	23	88	53	5	13	56	77
Juncus trifidus	29 (3)	50	8	45	40	1	36	20	56
Elyna Bellardi	7	45	4	53	12	»	3	»	22
Selaginella selaginoides	4	45	14	40	17	»	2	4	66
Equisetum variegatum	2 (2)	28	5	20	19	3	1	16	15
— pratense	1 (5)	23	5	18	35	10	»	40	50
Trisetum spicatum	7	18	2	22	7	»	3	4	35
Cardamine pratensis	1	11	5	13	8	»	»	8	26
Galium boreale	1	37	48	26	60	»	3	4	73
Equisetum arvense	1	20	20	10	»	»	»	40	4
Agrostis canina	18 (1)	67	75	95	96	1	46	60	89
Salix glauca	3	19	30	1	»	»	2	»	2
Deschampsia flexuosa	2	25	90	18	53	»	6	16	64
Vaccinium uliginosum	4 (+)	54	75	8	80	»	8	»	14
Viola palustris	»	1	25	»	»	»	»	»	3
Geranium sylvaticum	»	+	25	»	»	»	»	»	2
Agrostis tenuis	»	3	23	»	1	»	»	»	5
Galium verum	+	2	20	20	4	»	1	»	10
Gnaphalium supinum	»	1	19	»	»	»	»	»	»
Taraxacum officinale	»	+	18	1	3	»	»	»	1
Calluna vulgaris	»	1	12	4	85	»	»	»	2
Sibbaldia procumbens	»	»	12	»	»	»	»	»	»
Rumex acetosa	1	6	12	»	»	1	2	12	6
Luzula multiflora	»	6	10	5	15	»	»	»	2
Hierochloë odorata	»	»	9	»	»	»	»	»	»
Vaccinium Myrtillus	»	»	7	»	»	»	»	»	»
Alchemilla alpina	1	»	4	»	»	»	»	»	»
Leontodon autumnalis	»	»	6	»	»	»	»	»	»
Alchemilla minor	»	»	5	»	»	»	»	»	»
Rubus saxatilis	»	»	2	»	»	»	»	»	»

Snow-Covering (cfr. the text).

Thrasaborgir				Lækjamót		Norðtunga			Arnavatnsheiði				
e	a	b	c	a	b	a	b	c	a	b	c	d	e
»	»	»	»	»	»	»	»	»	13	»	»	»	»
»	»	»	»	11	»	»	»	»	3	»	»	»	»
»	»	»	»	»	»	»	»	»	12	»	1	»	»
»	»	»	»	35	»	»	»	»	7	»	»	»	»
»	»	»	»	8	»	»	»	»	36	»	»	»	»
»	»	»	»	23	»	»	»	»	34	9	4	»	»
»	»	»	»	43	24	»	»	10	45	6	10	1	»
»	»	»	»	30	84	»	»	»	41	26	26	»	»
»	1	2	»	50	28	4	»	2	43	10	9	»	»
»	9	22	»	54	62	32	»	»	65	63	50	1	»
1	2	24	»	47	62	48	2	»	69	44	62	3	»
15	»	»	»	54	88	88	9	»	49	8	11	4	»
1	2	6	2	46	30	64	38	10	57	42	12	»	2
54	40	82	74	1	54	72	70	60	»	47	70	84	84
38	96	96	96	8	66	64	7	»	59	86	87	88	100
28	31	88	54	33	98	76	61	24	78	98	96	68	54
97	7	60	72	1	92	84	72	16	28	93	98	75	50
68	5	86	74	32	92	96	83	48	11	77	88	39	62
5	9	60	12	24	94	80	78	60	5	76	88	93	»
30	»	58	4	26	46	68	53	20	4	18	37	28	»
8	4	42	»	9	52	60	27	6	43	40	48	5	»
2	»	»	»	12	86	84	15	»	6	32	45	1	»
12	»	30	24	9	56	40	5	»	»	18	66	29	»
»	»	28	»	3	30	»	»	»	2	18	76	8	16
16	»	»	»	3	38	52	9	18	»	»	»	»	»
2	»	»	»	12	20	16	6	»	7	11	27	»	»
24	»	»	»	3	38	»	»	»	»	»	10	1	»
85	»	74	76	»	»	72	78	40	»	»	»	»	»
1	»	6	2	3	30	16	3	»	1	26	38	28	66
71	»	92	88	8	80	92	72	60	»	8	40	55	88
2	»	»	2	»	18	»	»	»	8	55	37	55	88
99	»	64	98	»	»	16	80	98	»	»	6	97	74
99	1	4	58	»	68	88	85	30	4	76	72	85	50
21	»	»	48	»	»	»	8	2	»	»	»	24	26
17	»	»	8	»	»	»	5	»	»	»	»	93	2
45	»	2	30	»	»	12	19	18	»	»	»	21	»
15	»	2	2	»	»	»	53	8	»	»	»	31	»
»	»	4	50	»	»	»	»	»	»	»	»	8	36
23	»	»	10	»	»	»	8	2	»	»	»	20	30
59	»	»	»	28	»	»	»	»	»	»	»	12	22
»	»	2	»	»	»	8	4	1	8	»	1	15	27
15	»	»	2	»	20	12	32	8	»	»	»	»	»
»	»	»	»	»	»	»	1	»	»	»	»	28	16
30	»	»	6	»	»	»	»	»	»	»	»	7	»
»	»	»	14	»	»	»	»	»	»	»	»	»	6
4	»	»	4	»	»	»	»	15	2	»	»	»	13
4	»	»	8	»	»	»	»	»	»	»	»	»	»
5	»	»	4	»	»	»	»	1	»	»	»	»	»

There are, however, a few interesting deviations from the rule.

Thus *Calluna vulgaris* is of common occurrence in the mo at Bjørk. At Lýngdalur it is absent, or practically absent from the mo, whereas it occurs very abundantly in the snow patches. At Thrasaborgir it occurs neither in the mo nor the geiri.

Deschampsia flexuosa occurs both in the mo and the geiri in the south country; in the south-west, the north, and the highland tracts it is either entirely absent or occurs only in scattered growth in the mo, whereas it is very abundant in the geiri (and forest).

Thalictrum alpinum is a mo plant in the south country but shuns geiri; in the south-west and north country it is still a mo plant, but here it is also met with in the more snow-covered types of vegetation as forest and geiri.

It seems natural to suppose that these deviations are due to differences in temperature.

Vaccinium uliginosum is another interesting example. Its F.-percentage varies as follows in the scale of snow-covering. In I a (mosathembur) it has an average F.-percentage of 0.5, in I b (mellar) 4. Class II, i. e. the mo, has an average F.-percentage of 54 and class III 75. The species is thus a pronounced geiri plant though with strong tendencies towards the mo. At Bjørk it plays a prominent part in the mo, especially the Arctostaphylos mo, while the Elyna mo is less favourable. In the mo at Lýngdalur it is but sparsely represented, while it is dominant in geiri. The same applies at Thrasaborgir. In the highland tracts, at Lækjamót and Norðtunga, it is not only peculiar to the areas with a deep snow-covering, it also occurs with a high F.-percentage in the mo. On mellar it does not occur, however.

These peculiarities must no doubt be put down to differences in the scale of snow-covering between the south country on the one hand and the rest of the country on the other. In the highland tracts and the north country the snow-covering is more constant than in the south country, the mo of which is sometimes covered with snow, sometimes bare.

Table 30 shows the distribution of the species groups in the scale of snow-covering. The signatures are the same as in table 29. The average values are given at the end of the table. It appears from the table with all desirable plainness that the A percentage is highest in the class most bare of snow, i. e. in

I a, (mosathembur); from here its value decreases until it attains its minimum together with the maximum of the E percentage in the class with the deepest snow-covering. The proportion of the average F.-percentages of the two species groups in the class most bare of snow is as 83 to 17, in the class with the deepest snow-covering as 34 to 66.

The variations in the distribution of the individual sub-groups are closely correlated to the variations in the distribution of the main groups. A 3 attains its highest value in the highest class and thence the F.-percentage decreases steadily as we pass downwards through the classes. It shows the following change: $70 \rightarrow 48 \rightarrow 35 \rightarrow 20$. The maximum of the A 2 species lies lower in the scale, that of the A 1 species still lower.

The maximum of the latter group is in class II, corresponding to the normal snow-covering of the country. In this class the E species, too, attain their maximum, though not a very pronounced one. The lower E sub-groups, E 3, E 2, and E 1 all have their maxima in class III, corresponding to the fact that the species thrive best where there is a deep and constant snow-covering throughout the winter. Here E 3 is most abundant, E 2 is somewhat less dominant, and E 1 occurs only sparsely.

Thus to the 3 classes of snow-covering there corresponds a vegetation quite definitely stamped by its environment. In class I it consists chiefly of A 3 species, less of A 2 species, in class II of A 2, A 1, and E 4 species, and in class III of E 3, E 2, and E 1 species.

The snow-bare vegetation of Iceland thus consists of species with a pronounced northern distribution, the vegetation with a constant snow-covering of species with a pronounced southern distribution, and the vegetation with a normal snow-covering is composed of species belonging to tracts the climate of which corresponds to that of the country.

Conditions in the individual localities entirely confirm the facts stated above, both in respect of the quantitative distribution in the main groups and the position of the maximum in the individual subgroups. A decrease in the amount of snow will always tend to render the vegetation more arctic, an increase will render it more southern.

This distribution is especially very plainly seen in the highland scale. As everywhere else A 3 attains its maximum in the highest class, which is relatively unfavourable to A 2. The maximum of this group is the second or third highest class, while A 1 does not attain its maximum until yet another degree lower in the scale. In the lowest class there is a rise in the A percentage which would seem to suggest that too large an amount of snow restricts the growth of the southern species but promotes that of the arctic species. The *Salix herbacea*, *Sibbaldia procumbens* and *Anthelia* societies previously cited must be assumed to be a development resulting from this fact.

The change in the proportion of A and E species as we pass from snowbare to increasingly snow-covered vegetations is the same whether expressed in frequency sum numbers or in the species numbers alone. This is very plainly evident from the species groups spectra in table 8 which have been calculated from Ingimar Óskarsson's species lists from Vestfirðir. The series melar → heather and mo → herbfield and birch copse corresponds to the above-mentioned snow-covering classes I—II—III. The percentage amounts of A, A 3, and E 3+2+1 species in the various groups of vegetation are as follows:

	A per-	A 3 per-	E 3+2+1
	centage	centage	percentage
Highland melar	82	24	4
Lowland melar	60	22	23
Heather and mo veg.	50	13	32
Herbfield and birch copse	23	7	48
Hot springs	»	»	75

Even though the values do not coincide with those given in table 30, the correspondence in the variations of the series of figures is beyond doubt.

A comparison between the species group spectra for the various types of vegetation, partly in the different parts of the country, partly at different heights above sea-level, will be of interest.

Thus the melar vegetation in the south country has a lower A percentage and A 3 percentage, but on the other hand a higher E 3+2+1 percentage than the corresponding vegetation in the north country and the highland tracts. The numerical values are as follows.

	A percentage	A 3 percentage	E 3+2+1 percentage
Melar in S. Icl.	60	36	11
- - N. Icl.	75	52	2
- highland	81	55	»

The corresponding figures for the mo respectively in South Iceland, South-West Iceland, and North Iceland at c. 100 m above sea-level are as follows.

	A percentage	A 3 percentage	E 3+2+1 percentage
South Iceland	33	18	34
S. W. Iceland.....	48	25	19
North Iceland	64	39	11

At various heights above the sea the figures in the south country are as follows.

	A percentage	A 3 percentage	E 3+2+1 percentage
At 100 m	33	18	34
- 200 m	50	29	25
- 3—400 m	58	33	25
- 500 m (highl.)....	71	41	3

The figures for the geiri vegetation in the south country are as follows.

	A percentage	A 3 percentage	E 3+2+1 percentage
At 200 m	20	12	52
- 3—400 m	36	22	43
- 500 m	44	24	35

For the mosathembur vegetation.

	A per-	A 3 per-	E 3+2+1
	centage	centage	percentage
At 100 m (the Elyna mo).....	52	30	18
- 200 m (the mosathembur veget.)	74	55	5
- 300 m - - -	90	83	3
- 400 m - - -	100	100	»

The figures all point in the same direction; where the temperature conditions are most favourable, the southern species are most abundant, where the cold is predominant, the northern species abound. This relation remains

the same if the species numbers alone are employed instead of the frequency numbers.

The occurrence and quantitative distribution of the species groups in the Icelandic types of vegetation is determined throughout by the temperature conditions prevalent in the locality. The prolonged low temperature prevalent in the highlands and the north country but especially in localities where the snow is blown away in the winter, promotes the growth of northern but restricts the growth of southern species, while a prolonged high temperature, as it occurs in the lowlands and the south but especially wherever the ground is covered with a deep and constant layer of snow, restricts the growth of northern but promotes the growth of southern species. This is abundantly confirmed by the vegetation around the hot springs.

We are thus fully justified in regarding the species groups as indicators of environment, and the species group spectra will then prove an important guide in a more precise analysis of environment. Under the treatment of the distribution of the species groups in the Icelandic scale of moisture, the spectra furnished important holds for an examination of the physical conditions. The legitimacy of the above-stated considerations is further confirmed by the distribution of the species groups in the scale of snow-covering, in the types of vegetation of the different parts of the country and the altitudinal zones, and by the vegetation around the hot springs.

In two areas, partly in the geiri and partly in the flói, on soil covered respectively with snow and with water, the E species are unusually abundant. In both places the winter temperature must be supposed to be almost the same, at or below zero. When the snow has melted in the geiri, the heat that is left will directly benefit the plants. In the flói, on the other hand, a great deal of the heat is latent in the water which still covers the vegetation, consequently the result will be a relatively low summer temperature. The flói is thus warm in the winter but cold in the summer, while the geiri is warm both in the winter and the summer. The result will be that in both places the species group spectrum is characterised by a high E percentage; on the water-covered soil it is 72, on the snow-covered soil 66. The difference in the summer

temperature appears especially in the E group spectrum in that the lower E sub-groups occur abundantly on snow-covered soil, but are entirely absent from water-covered soil. The E 2 and E 1 species are such as require a high temperature to be able to thrive, and this requirement is only satisfied in geiri and forest.

The A group spectrum shows a peculiar difference between the two types of vegetation. The A percentage is 34 in the geiri, 28 in the flói. In the flói 20 p. c. of these species are A 1 species, and only 8 p. c. are A 3 and A 2 species, while in the geiri the A 1 percentage is only 4, and the sum total of the A 3 and A 2 percentages is no less than 30.

The high A 3 percentage in the snow-covered vegetation and the low A 3 percentage in the water-covered vegetation must be assumed to be a consequence of difference of stability in the covering medium. In the flói the water is always present, hence the vegetation is never exposed to severe cold. Thus a condition necessary for the growth of A 3 species is not present.

Compared with the water in the flói, the snow in the geiri is less stable. A hard frost may set in before the first snowfall, and frost in the night may affect the vegetation after the snow has melted. This provides a possibility for the growth of the A 3 species, hence compared with water-covered soil the A 3 percentage is high, but compared with snow-bare soil or a vegetation with a normal snow-covering, it is comparatively low. The A 3 percentage is higher in geiri than in forest, respectively 23 and 14, which further confirms the above considerations.

Thus the difference between the species group spectra for water-covered and snow-covered vegetation is as follows. The species in the species group spectrum of the water-covered vegetation are largely concentrated in the central part of the spectrum with a marked dominance of E species, corresponding to a favourable and fairly stable winter temperature, and only a slight difference between the winter and summer temperatures. The species in the species group spectrum of snow-covered soil, on the other hand, though also showing a preponderance of E species, are distributed over the entire scale in consequence of a relatively high winter and summer temperature, and greater instability in the winter.

As previously mentioned, the species group spectrum for the

Subularia flag, the water-covered vegetation rich in Th, corresponds closely to that of the flói: concentration of the species in the central part, and preponderance of the E species.

The treatment of the distribution of the species groups and the life-forms in the scale of moisture showed that moderately moist soil (*jaðar*) caused a relative maximum of E species, hemicryptophytes and therophytes. This was the case with the vegetation on a gently sloping surface with even transitions from one type of vegetation to another. However, on moderately moist soil there occurs a series of types which, physiognomically, are rather different, both mutually and in relation to the *jaðar*, but which, on close inspection, prove to be possessed of the peculiarities of the *jaðar* vegetation, though in varying degree, viz. a relatively high H percentage and Th percentage. Of these types the valllendi and flag vegetations have so far been examined. The first of these types develops on the flat cones deposited by the rivulets of melting snow on flat ledges. The valllendi soil is thus saturated with water until the last snow has melted, i. e. until the *geiri* is bare of snow. In the flag, conditions are otherwise. If it receives any water at all while the snow is melting, it is at most as long as there is snow on the mo. The bare soil of the flag is thus exposed to the effects of the frost (night frost) much longer than the valllendi, which is furnished with fresh water daily. Hence it is hardly accidental that the E species are more dominant in valllendi than in flag. The E percentages for valllendi, *jaðar*, and flag are respectively 75, 53, and 42.

The Distribution of the Life-Forms in the Scale of Snow-Covering.

Since differences in respect of snow-covering only appear in areas not affected by ground-water, where, as previously mentioned, Ch, H, and Th are the dominant life-forms, it is principally the relation of the snow to these which is of interest. Table 30 shows the biological spectra of the various classes of snow-covering in the localities examined by me. At the bottom of the table are given the mean values for all the investigations.

It appears from the table with all desirable plainness that Ch are more abundant on snow-bare soil than on soil with a normal snow-covering, and more abundant there than where the soil has a constant snow-covering. For H the case is re-

TABLE 30. The Distribution of Species Groups and Life Forms in the Scale of Snow Covering.

1. Björk. 2. Lýngdalur. 3. Thrasaborgir. 4. Lækjamót.
5. Nordtunga. 6. Arnarvatnsheiði. 7. Average.

	Points sum	Number of species	Density of species	A	E	A3	A2	A1	E4	E3	E2	E1	Ph.	Ch	H	G	HH	Th
1a ...	4536	29	11.4	52	48	30	11	11	30	11	5	2	»	28	56	16	»	»
b ...	4096	30	13.6	33	67	18	9	6	33	13	21	0.3	»	39	47	14	»	0.2
Ia 2a ...	1228	9	2.4	75	25	55	18	2	21	1	4	»	»	10	41	48	»	»
Ib b ...	3852	18	5.5	60	40	36	19	5	30	10	1	0.2	»	43	39	18	»	»
(Ia-II) c ...	860	27	8.6	57	43	35	14	7	27	10	6	»	»	23	51	26	»	0.5
II d ...	6644	34	13.3	50	50	29	10	11	25	14	10	1	»	26	56	17	»	0.3
III e ...	7418	25	10.6	20	80	12	3	5	28	26	24	2	»	35	55	10	»	»
Ia 3a ...	1340	9	2.2	91	9	85	7	»	6	»	3	»	»	57	8	35	»	»
II b ...	1924	22	9.6	58	42	33	16	9	17	17	8	0.2	»	25	56	18	»	0.2
III c ...	2064	31	10.3	36	65	22	11	3	21	27	16	0.2	»	34	49	17	»	0.2
Ib 4a ...	2058	27	6.9	75	26	52	16	7	24	1	1	0.2	»	45	47	5	»	3
II b ...	3480	39	17.4	64	36	39	18	7	25	7	4	0.1	»	35	49	14	»	2
II 5a ...	1392	31	13.9	48	52	25	15	8	33	9	10	»	»	29	55	16	»	0.3
III b ...	4316	43	10.8	30	70	14	10	5	27	28	11	4	»	17	70	14	»	»
(III) c ...	1276	23	6.4	25	75	13	10	3	17	46	11	1	»	8	75	17	»	»
Ib 6a ...	4748	27	7.9	81	19	55	20	6	19	»	»	»	»	52	36	10	»	2
II b ...	5664	32	11.3	70	30	43	24	3	30	1	»	»	»	48	37	15	»	1
II c ...	7184	35	14.4	71	29	39	25	7	24	4	»	»	»	38	47	15	»	0.3
III d ...	3892	32	13.0	44	56	24	13	7	21	27	6	2	»	31	53	16	»	0.2
III e ...	2000	21	10.0	48	52	34	13	1	24	23	5	»	»	35	43	22	»	»
7. Ia ...	2568	9	2.3	83	17	70	13	1	14	1	4	»	»	27	40	33	»	»
Ib ...	10,658	24	6.8	72	28	48	18	6	24	4	0.5	0.1	»	47	41	11	»	2
II ...	26,288	32	13.3	60	40	35	18	9	26	9	5	0.2	»	34	50	16	»	1
III ...	20,966	29	10.2	34	66	20	10	4	23	30	12	1.5	»	27	58	16	»	0.1

versed, this group occurs in greatest quantity on soil with a constant snow-covering, while the Th group behaves like Ch.

If instead of the values for frequency we use the species number alone, the result will be the same. The Th percentage for snowbare soil, soil with a normal snow-covering, and soil with a constant snow-covering at Vestfirðir, calculated from Ingimar Óskarsson's species lists, is respectively 37, 24, and 20.

Hence the following rule applies to the distribution of the life-forms in the Icelandic scale of snow-covering. On the most

snow-bare soil Ch thrive best, the deeper the snow-covering the more does the Ch percentage decrease, while, on the other hand, the H percentage increases, and where the snow-covering is deepest, H play the most prominent part. This distribution must be regarded as a consequence of the geographical distribution of the life forms. Ch, the arctic life-form, thrive best where the cold has the strongest effect, while the more temperate life-form, H, shows a preference for conditions in which there is the greatest protection from the cold.

From this rule of the distribution of the life-forms in the Icelandic scale of snow-covering there is an interesting, though merely apparent, deviation, as will appear from a close investigation of conditions in the individual localities. In the highlands the rule applies throughout, the slighter the snow-covering, the higher the Ch percentage (though in the very lowest class there occurs an increase), and in the lowlands too it holds good if we consider the relation between mellar and mo, i. e. between snow-bare and snow-covered soil. In other respects conditions in the lowlands seem to go against the rule, Ch playing the most prominent part where the snow-covering is deepest and of the longest duration, whereas this group decreases when the depth of the snow-covering decreases. The Ch percentage in the Elyna mo, the comparatively snow-bare formation at Björk, is 28, whereas, in the Arctostaphylos mo, the relatively snow-covered formation, it is 39. In the mo at Lýngdalur the Ch percentage is 26, in the geiri 35, and in mosathembur only 10. At Thrasaborg the values for mo and geiri are 25 and 34 respectively.

This difference in the distribution of Ch in the highland and the lowland scale of snow-covering is due to the fact that the Ch vegetation in the lowlands consists especially of E species, whereas, in the highland tracts, it consists of A species. This disagreement thus handsomely confirms the distribution of the species groups in the scale of snow-covering.

Raunkiær examined the variations in the biological spectra in sections from southern towards northern regions (1908, 1911) and showed that some life-forms, Ph, K, and Th, decrease in quantity, while others, Ch, increase and others again, H, undergo no appre-

ciable change, are indifferent. Passing upwards from the level of the sea to the snow-line in a mountain district, we find the same changes.

In Iceland the same holds good for the variation according to altitude: The H percentage remains unchanged throughout the altitudinal zones, the arctic life-form Ch increases rapidly, while the southern life-forms, Pt, Ph, G, HH, and Th, decrease in the same proportion.

These changes in the life-form spectra are connected with, or caused by, a decrease in the warm temperature of the summer and an increase in the cold temperature of the winter. The summer temperature grows lower and the summer of shorter duration, while, on the other hand, the winter grows longer and more severe the further northward we go.

If we calculate the biological spectra for the Icelandic types of vegetation and compare the spectra for the types on snow-bare soil, on soil with a normal snow-covering, and on soil with a constant snow-covering, we get the same variations as above on passing from arctic towards temperate regions or from the snow-line towards the level of the sea.

The result will be the same whether we base our calculations on the number of species or on the number of individuals, i. e. on the frequency sum.

There is no reason to believe but that, in this case too, it is the temperature conditions which determine the occurrence and development of the life-forms. The temperature conditions favourable to the arctic species are due to the fact that the snow is blown away so that the cold can act with its full force on the vegetation with the result that southern types cannot survive, while arctic types thrive. Where the snow-covering is deep and constant, the case is reversed; here the environment will be unfavourable to arctic but favourable to temperate types because the snow-covering will prevent the extreme variations in temperature from reaching the vegetation.

Hence, under conditions where the external factors are not easily observable, the individual life-forms may with full justice be employed, as above, as indicators of environment. Thus, in Iceland, many Ch will indicate severe cold, many Ph, K, and Th relatively favourable temperature conditions.

From a scientific point of view, as a means of checking life-

forms, it will be of interest to have another system of indicators of environment. In the present treatise the geographical distribution of the individual species has been employed as an indicator of environment. A species with a pronounced southern distribution will more certainly indicate a high temperature than a more northern species. The more southern species there occur in an area, and the more prominent the role they play, the more probable will it be that the temperature conditions are favourable. Reversely, it must be supposed that a preponderance of arctic species indicates severe cold. The proportion of southern and arctic species in an area will therefore indicate the temperature conditions of that area.

In a previous chapter the species groups were dealt with in more detail. At the outset it might be anticipated that the species groups would be more sensitive indicators than the life-forms, and it might be claimed that the two systems of indicators should lead to the same result. An inspection of the tables will show to how great an extent this is the case. A change of environment causing an increase of the Ch percentage will likewise cause an increase of the A percentage, and numerically this increase will be greater than the Ch increase.

Table 31 shows the life-form and species group spectra for a series of areas in which the conditions of environment are most clearly illustrated. The localities are arranged in groups of 3 each. The top group 1, comprises the land spectra for Denmark, Iceland, and North Greenland, group 2 the Icelandic zone spectra for the lowlands and the upper and lower zones of the highlands respectively, group 3 various zone spectra from Vestfirðir, for the 0—100 m zone, the 2—300 m zone, and the 3—400 m zone respectively, group 4 shows vegetation spectra for snow-bare, normally, and constantly snow-covered vegetation in the same locality, and group 5, finally, gives the mean values for the formation spectra of the various classes of snow-covering. Within each group the coldest area, a, is given first, the warmest, c, last.

A closer inspection of the table will show that, compared with the b spectra, all the a spectra have a high Ch percentage, A 3 percentage, and especially a high A percentage, while the c spectra, on the other hand, have a high (Ph + K + Th) percentage and (E 3 + E 2 + E 1) percentage. The amount of H and (A 2 + A 1 + E 4) species is relatively unaffected by changes in temperature in any

TABLE 31. Agreement in Variation of Biological Spectra and Species Group Spectra (cf. Text).

	Ch %	H %	Ph K Th %	A %	A 3 %	A 2, A 1, E 4 %	E 3+2+1 %
1. N. Greenland	a	35	50	15	»	»	»
Iceland	b	15	52	33	»	»	»
Denmark.....	c	3	50	47	»	»	»
2. Iceland, 8—1200 m. above sea.....	a	34	53	13	80	58	38
— 3—800 m.....	b	21	53	26	52	20	49
— 0—300 m.....	c	15	52	33	40	15	41
3. Vestfirðir, 4—500 m above sea....	a	43	50	7	93	50	50
— 2—300 m.....	b	31	51	18	68	27	56
— 0—100 m.....	c	17	52	31	41	15	47
4. Snow-bare vegetation Vestfirðir....	a	37	52	11	71	32	54
Normally snow-covered vegetation . b		24	55	21	50	13	55
Constantly snow-covered vegetation c		20	51	29	28	7	45
5. Snow-covering class I.....	a	47	41	12	72	48	47
— - II.....	b	34	50	16	60	35	51
— - III.....	c	27	58	15	34	20	36

direction; in all the spectra these two groups constitute about half the material.

The effect of a change in temperature is thus the same in both systems of indicators, but it is most marked in the species group system.

Hence, when we have elsewhere in this treatise employed the species group and life form spectra when considering the external factors prevalent in the formations, this is quite justifiable; a spectrum, particularly a species group spectrum, will thus be an important guide in the determination of the external factors which are of importance for the vegetation.

Variations in the density and number of species in the scale of external factors bring to light interesting relations. In the 4 classes of snow-covering I a, I b, II, and III, the mean density of species is respectively 2.3, 6.8, 13.3, and 10.2, and the mean number of species is 9, 24, 32, and 29; in the 7 classes of moisture the mean density of

species from class I to class VII is given by the following values: 8.3, 12.7, 14.3, 13.2, 11.1, 7.9, and 1.8 and the mean number of species in the corresponding classes by 25, 32, 36, 39, 33, 19, and 5. It applies both to the number and density of species that they attain a maximum in both scales of external factors, whence they decrease more or less in both directions. The position of this maximum corresponds to the conditions of environment normally prevalent in the country, and practically coincides for both series of figures. The maximum for the scale of snow-covering lies in class II, corresponding to the mo, for the scale of moisture it lies in classes III—IV, corresponding to moist mo and jaðar. These types of vegetation must be regarded as the climax vegetation of the country.

The rule thus seems to hold good that those parts of the country where the environment is typical of the country and which, therefore, bear the climax vegetation of the country, have the vegetation which is richest and densest in species. No matter in what direction the external factors are changed, whether in the direction of greater drought or greater moisture, or in the direction of a deeper or a slighter snow-covering, the result will always be a diminution both of the number and of the density of species, and the greater the change of environment, the greater the diminution.

Our investigation of the distribution of the species, species groups, and life-forms in the formations, arranged according to increasing prevalence of one and the same external factor, has herewith been brought to a close as far as the Icelandic scales of moisture and snow-covering are concerned. Besides extending the investigations to an increased number of external factors, it will likewise be appropriate to divide the flora into groups according to the distribution of the species from Atlantic to more continental regions. It would also seem of interest to divide the flora into groups according to the geographical distribution of the genera, as well as according to the quantitative distribution of the species within their areas. Judging by the investigations given above, such an extension of view-points would lead to a more thorough understanding of the distribution of plants in Iceland, the knowledge of which is essential partly for the question of the genesis

of the Icelandic species, partly for the question of the cultivation of the various Icelandic types of vegetation.

Other questions of decisive importance in studies on the distribution of the species in the scales of external factors are partly the question of equidistance in division, and partly the question of the determination of the number of external factors bearing on plant distribution.

As far as the first question is concerned, in formations with low density of species, the line between two formations is most naturally drawn at the physiognomic boundary line between the two formations, and the areas selected for examination should as far as possible be laid in the middle of the formation. It is possible that the distance between the various localities examined will not in this way become an exact expression of physical equidistance between the localities, or the formations, but merely of ecological equidistance; but since the investigation is primarily ecological, it will suffice if the requirement of ecological equidistance is satisfied, even though physical equidistance would have been desirable.

Where we are concerned with the investigation of formations with many species, the requirement of ecological equidistance between the localities examined will be considerably more difficult to satisfy. The present treatise deals principally with formations of this kind, and the examination of them was made in the following way. On a gently sloping surface the investigator passed so far up and down from one locality that the vegetation had changed appreciably; the second locality was then examined here, whereupon the third locality was chosen and examined in the same way.

It is possible that the distances between the localities examined are unequal both physically and ecologically; so much is certain, however, that the sequence of the localities examined expresses a constantly increasing change of environment. If this is the case, however, we have in the proportion of the species points of species occurring principally above, and species occurring principally below, the formation in question an aid in determining the question of ecological equidistance between the formations.

Another question of equal importance is the question of the determination of the number of plant-distributing factors. This question, however, is only topical in a plant covering rich in species and of uniform physiognomy. If such a plant covering is examined

by means of Raunkiær's circling method, the flora lists of the individual random samples will furnish a point of departure for the consideration of this subject.

This question, as well as the others referred to above, I have, however, been obliged to leave for future consideration, partly for lack of time, partly for want of suitable material. A few more questions, thus some investigations on the acidity of some types of Icelandic vegetation, and some reflections on the relation between plant geography and farming, will be dealt with briefly below.

Determinations of the acidity of the soil were made simultaneously with the investigation of the vegetation. The mode of procedure in taking samples of the soil and determining the degree of acidity was that described by Carsten Olsen (1921). For practical reasons the investigation was only made at Björk, on Lýngdalsheiði, and on Arnarvatnsheiði.

For the various types of vegetation in the above-mentioned localities the acidity expressed in p_H was as follows:

At Björk

Elyna mo	6.5, 6.5	average 6.5
Arctostaphylos mo	6.5, 6.5, 6.4	— 6.5
Calluna-Empetrum mo .	6.4, 6.3	— 6.4
Jaðar	6.0, 6.0	— 6.0
Salix mýri	6.0, 5.7, 5.7	— 5.8
Betula nana mýri	5.7, 5.6, 5.2, 5.2	— 5.4
Koenigia flag	6.6, 6.3	— 6.5

On Lýngdalsheiði

Mosathembur	6.5, 6.4, 6.3, 6.3	— 6.4
Melar	6.3, 6.3, 6.2, 6.2	— 6.3
Mo	6.4, 6.4, 6.4, 6.4, 6.3	— 6.3
»	6.2, 6.2, 6.2, 6.2	
Valllendi	6.3, 6.2, 6.1, 6.1, 5.7	— 6.1
Jaðar	6.0	— 6.0
Salix mýri.....	5.3	— 5.3
Betula nana mýri	5.3, 5.1, 5.1, 5.0, 5.0, 4.8, 4.8	— 5.0
Geiri	6.1, 6.1, 6.0	— 6.1

On Arnarvatnsheiði

Melar	6.9, 6.8, 6.7, 6.6, 6.6	— 6.7
The level mo	6.8, 6.8, 6.4, 6.3, 6.2	— 6.5

The knolly mo	6.8, 6.8, 6.4, 6.2	average 6.5
Jaðar	6.2, 6.2, 6.1, 6.1	— 6.2
Mýri	6.3, 6.1, 6.0, 5.9, 5.9, 5.6	— 5.9
Geiri (Geranium belt) ...	6.5, 6.4	— 6.3
— (bottom veget.)	6.3, 6.1	—

Thus the Icelandic soils all seem to be slightly acid; no degrees of acidity above the neutral point were measured, nor did any very strongly acid soils occur. The highest value measured in p_H was 6.9, the lowest 4.8; according to C. Olsen, the corresponding values for Denmark are respectively 8.0 and 3.4. There is this connection between the moisture of the soil and its degree of acidity that increasing moisture produces increasing acidity, i. e. decrease in p_H value. In mellar p_H is about 6.7, in the mo 6.3—6.5, in jaðar 6.0—6.2, and in mýri 5.2, 5.5, and 5.9. An increase in the depth of snow-covering shows the same relations: in mellar p_H is 6.7, in mo 6.3—6.5, and in geiri 6.1—6.3.

The investigations described in the present treatise are not only of phytogeographical and botanical interest, but would also seem to have some bearing on practical matters, partly in agricultural research, and partly more directly in farming. Since, however, these matters have not been subjected to special investigation and are outside the scope of the present treatise, I shall merely make brief mention of a couple of questions connected herewith.

Under the treatment of the vegetation the appearance of the surface in the individual types was described. A comparison between this and the species group spectra reveals the following facts. When the E percentage is high, i. e. when the vegetation consists of southern species, the surface is always level, without any formation of knolls, whether the high E percentage is caused by a deep layer of snow or by the soil being covered with water. If, reversely, the vegetation consists mainly of arctic species, solifluction is always seen. If the vegetation consists of an equal mixture of A and E species knolls will always be met with.

This difference between the types of surface connected with the different types of vegetation must be assumed to be a result of the same external factor that determines the differences in vegetation, in this case the cold. In geiri and flói (snow-patch and

swamp) the soil is protected from the frost and therefore even; in mo, jaðar, and (mýri) the frozen surface will crack in the spring, as in Denmark, and form greater or smaller polygons which will furnish a foundation for the formation of knolls. How this latter takes place is still uncertain. It seems natural to suppose that it is due to the action of frost which may also be observed in Denmark when clayey or boggy soil freezes. On such soil, which has been exposed to a long period of frost, the surface will be observed to have been raised in various ways, and the frozen crust will be seen to consist of alternate layers of ice and frozen earth. When the water freezes the whole mass of soil expands upwards, either in the shape of a large cake or as a radiating system of branches of ice and earth. The greater the moisture and the longer the action of the frost, the more marked is this phenomenon. If the Icelandic formation of knolls is a result of the same forces, it may be anticipated to be most pronounced on moderately moist soil and in regions where frosts are frequent. And, as a matter of fact, the formation of knolls attains its handsomest development in jaðar in the highlands where precisely these two conditions are present.

According to this view the knolls (in mo and jaðar) should be a kind of "frost-baked earth-balls", for which the polygonal soil forms the point of departure. Frost is the agent and water the expanding factor which, on freezing to ice, changes the internal structure of the knoll from a relatively compact to a more porous state. In accordance herewith it will, in fact, be observed that the interior of the knolls is peculiarly loose, almost like flour.

If there is a continued formation of knolls it will, in regions much exposed to wind, become a starting point for solifluction. The surface of the knolls will break on the side exposed to the wind, and will at last be entirely eaten up by erosion. In areas where the action of the frost is relatively strong, as in melar, knolls will form the starting-point for solifluction.

The above considerations are merely of a sketchy nature. On the basis of general observations and the knowledge of external factors drawn from phytogeographical investigations I have attempted to correlate a series of peculiar soil phenomena. By a more methodical investigation of these in connection with a simultaneous phytogeographical investigation a better understanding of these factors, so important to Icelandic farming, might no doubt be gained

By the investigations described in the present treatise it has been shown how, within 3 areas in normal Icelandic physical conditions, favourable conditions for southern species are created, and thus a vegetation, the luxuriance of which permits of grazing or haymaking. These areas are either soils protected by water or by snow, or moderately moist soils which combine the favourable temperature conditions in winter of moist soils with the favourable temperature conditions in summer of dry soils.

The value of these areas for farming is caused by the fact that southern species and life-forms are larger and more vigorous, produce more matter than northern ones. Hence one of the chief aims in cultivating infertile areas should be to make such changes in the prevalent external factors that from being favourable to Ch they become favourable to H or G, according as the soil to be cultivated is comparatively dry or comparatively moist. The means employed for this purpose have been, partly a change in the conditions of moisture, partly in the conditions of nutrition. The results have, however, been very varied. The experiments have been most successful in the case of *mýri*, which it has been attempted to cultivate partly by irrigation, partly by draining. It is obvious that irrigation must result in favourable conditions for southern plants, since it increases the medium of protection against the winter cold. If the water is drained off in the summer, this will merely be a further advantage, since a lot of heat which would otherwise be latent in the water now becomes available for the plants. As a matter of fact, the transformation of *mýri* into irrigated *mýri* plays a prominent part in Icelandic farming.

The second way in which *mýri* may be transformed is by draining. In that way moist soil is transformed into moderately moist soil, *mýri* to *tún*. This change in moisture in connection with the addition of manure will have the effect of gradually replacing the sedge vegetation of the *mýri*, rich in G, by the grass vegetation of the *tún*, rich in H — a vegetation identical with the *jaðar* vegetation. Thus draining also produces a more southern vegetation, and the causes have previously been mentioned.

In the cultivation of the mo it has especially been attempted to transform it into *tún*. By treating the soil and adding manure to it, it has been attempted to make the *jaðar* plants grow here, and with some success. Hitherto, however, the object has been to transform a less southern to a more southern type of vegetation

but without a simultaneous change of the environment in the same direction. As a matter of fact the result is that "the tún burns" after cold winters and in hot summers, which is due to the fact that in the winter the plants miss the protection afforded by the jaðar soil, and in the summer its moisture.

Even if a transformation of mo to tún is not as profitable as the transformation of myri to tún, it must, however, on the whole be an advantage to farming. It is, however, questionable whether this is the right way of cultivating the mo. The investigations described in the present treatise have shown that water is the means of protection for southern plants on moist soil, while snow protects southern plants on the drier soils. Hence if a cultivation of the mo equally effective to that of the myri is desired, it should tend to utilise our knowledge of the importance of the snow-covering rather than aiming at the continued transformation into tún.

The importance of the snow-covering for the southern plants, and hence for the plants valuable to farmers, has long since been very thoroughly brought home to all parties concerned.

When the first Icelanders came to the island, c. 874 A. D., the country was covered with woods "milli fjalls ok fjäru". This however, is probably an exaggerated statement, says Thoroddsen, "but it is quite certain that the lowlands and valleys must have been more abundantly clothed with copse wood then than now, even if it must be assumed that large stretches of sandar, myrar, and lava fields were also then devoid of woods." Thoroddsen supposes, however, that when Iceland was first settled, the woods extended to an altitude of 600 m above sea-level, and that, at the beginning of the 10th century, they covered an area of 4—5000 sq. km. In 1911 the total wooded area had been reduced to 454 sq. km.

According to Helgi Jónsson (1900 p. 76), this great reduction has been caused by "reckless exploitation". But by destroying the trees, the constant snow-covering which was dependent on the presence of wood was also destroyed and, simultaneously, the luxuriant forest undergrowth which was again dependent on the snow-covering, and which formed, entirely or partially, the food of the farm animals. The great decline in old Icelandic culture, which numerically resulted in the population being reduced to half its former number, must no doubt be directly referred to the destruction of the woods. The correlation between these two factors has been outlined above.

APPENDIX.

Temperature Conditions in the Upper Soil Strata.

Apart from volcanic regions, where the upper soil strata receive heat from the interior of the earth, temperature conditions at the surface are practically determined by insolation. According to the extent of the cloud-covering, a greater or less amount of heat will reach the surface of the earth where part of it will be used for heating the air, another part for evaporation of the water in the soil, and a third part, finally, will heat the upper soil strata.

Investigations on the temperature conditions in the upper strata of the soil have been made at a series of stations in the most different climates. An accessible presentation of the questions relating to this subject will be found in Ramann, Bodenkunde 1911 and Hann, Lehrbuch der Meteorologie 1926, to which the reader is referred. A series of these investigations are, however, of such great phytogeographical interest in their bearing on the investigations described in this treatise that a brief abstract of the main results will be given in the following.

The investigations referred to originate partly, and especially, from Finland, and partly from Russia, and were made by Th. Homén (1894, 1896, 1897) J. Keränen (1920), and H. Wild (1897). The investigations comprise the daily and annual variations in temperature in snow and sandy soil, the temperature of the surface with and without snow-covering, and the daily variations in temperature in different kinds of soil, different in regard to structure, water-content, and plant-covering.

As an example of the daily variation in temperature in snow and sandy soil may be mentioned J. Keränen's investigations from Sodankylä of which an abstract is given in table 321—2. The temperature was measured every second hour throughout the 24 hours in the surface of the soil or the snow at different depths, in the case of the snow at depths of 4, 14, 24, and 44 cm. and in the case of the sandy soil at 10, 25, 40, 80, and 120 cm. The temperature of the air is given for each investigation.

The temperature of the surface of the snow or the sandy soil is determined by the proportion of insolation and radiation. Radiation is greatest in the night, hence the temperature decreases so that the lowest degrees of temperature occur just before sunrise; in

TABLE 32.

The Daily Variation in Temperature in Air, Snow, and Soil at Sodankylä (Finland, $67^{\circ} 22' N$, $26^{\circ} 39' E$).

1. Temperature measurements for snow, made 19–20 March 1917. After Keränen 1920, p. 92.
2. Temperature measurements for soil, made 25–29 June 1917, l. c. 196–197.

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	0	2	4	6	8	10	12	14	16	18	20	22	24	M	Diff.	
Air C°	$\frac{1}{\div 35.7}$	$\frac{1}{\div 37.9}$	$\frac{1}{\div 39.4}$	$\frac{1}{\div 40.4}$	$\frac{1}{\div 34.5}$	$\frac{1}{\div 20.4}$	$\frac{1}{\div 15.3}$	$\frac{1}{\div 12.7}$	$\frac{1}{\div 13.4}$	$\frac{1}{\div 16.9}$	$\frac{1}{\div 26.3}$	$\frac{1}{\div 31.9}$	$\frac{1}{\div 34.4}$	$\frac{1}{\div 27.6}$	$\frac{1}{27.7}$	
	$\frac{0}{\div 37.7}$	$\frac{0}{\div 38.9}$	$\frac{0}{\div 40.0}$	$\frac{0}{\div 40.1}$	$\frac{0}{\div 36.5}$	$\frac{0}{\div 24.0}$	$\frac{0}{\div 15.9}$	$\frac{0}{\div 14.4}$	$\frac{0}{\div 20.8}$	$\frac{0}{\div 28.1}$	$\frac{0}{\div 32.9}$	$\frac{0}{\div 34.7}$	$\frac{0}{\div 36.8}$	$\frac{0}{\div 30.2}$	$\frac{0}{25.7}$	
1. Snow	$\frac{0}{\div 4}$	$\frac{0}{\div 14}$	$\frac{0}{\div 19.0}$	$\frac{0}{\div 20.1}$	$\frac{0}{\div 21.0}$	$\frac{0}{\div 22.0}$	$\frac{0}{\div 22.5}$	$\frac{0}{\div 22.1}$	$\frac{0}{\div 20.1}$	$\frac{0}{\div 17.8}$	$\frac{0}{\div 16.6}$	$\frac{0}{\div 16.6}$	$\frac{0}{\div 17.5}$	$\frac{0}{\div 18.1}$	$\frac{0}{\div 19.0}$	$\frac{0}{5.9}$
	$\frac{0}{\div 24}$	$\frac{0}{\div 13.7}$	$\frac{0}{\div 13.9}$	$\frac{0}{\div 14.2}$	$\frac{0}{\div 14.7}$	$\frac{0}{\div 14.9}$	$\frac{0}{\div 15.1}$	$\frac{0}{\div 15.1}$	$\frac{0}{\div 14.9}$	$\frac{0}{\div 14.7}$	$\frac{0}{\div 14.5}$	$\frac{0}{\div 14.2}$	$\frac{0}{\div 14.0}$	$\frac{0}{\div 14.5}$	$\frac{0}{1.4}$	
	$\frac{0}{\div 44}$	$\frac{0}{\div 7.3}$	$\frac{0}{\div 7.4}$	$\frac{0}{\div 7.3}$	$\frac{0}{\div 7.5}$	$\frac{0}{\div 7.5}$	$\frac{0}{\div 7.6}$	$\frac{0}{\div 7.5}$	$\frac{0}{\div 7.7}$	$\frac{0}{\div 7.6}$	$\frac{0}{0.4}$					
Air C°	13.0	11.1	12.0	14.6	16.6	18.5	19.1	19.7	19.4	18.3	17.0	15.1	13.2	16.0	8.6	
	$\frac{0}{0 cm}$	$\frac{0}{10.4}$	$\frac{0}{9.5}$	$\frac{0}{9.8}$	$\frac{0}{16.0}$	$\frac{0}{20.9}$	$\frac{0}{29.4}$	$\frac{0}{31.5}$	$\frac{0}{30.9}$	$\frac{0}{27.5}$	$\frac{0}{21.7}$	$\frac{0}{16.5}$	$\frac{0}{12.9}$	$\frac{0}{11.0}$	$\frac{0}{19.9}$	$\frac{0}{22.0}$
2. Soil	$\frac{0}{\div 10}$	$\frac{0}{16.0}$	$\frac{0}{14.7}$	$\frac{0}{13.7}$	$\frac{0}{12.8}$	$\frac{0}{13.0}$	$\frac{0}{14.6}$	$\frac{0}{17.1}$	$\frac{0}{19.0}$	$\frac{0}{20.0}$	$\frac{0}{20.1}$	$\frac{0}{19.3}$	$\frac{0}{17.9}$	$\frac{0}{16.6}$	$\frac{0}{16.5}$	$\frac{0}{7.3}$
	$\frac{0}{\div 25}$	$\frac{0}{14.6}$	$\frac{0}{14.3}$	$\frac{0}{13.7}$	$\frac{0}{13.0}$	$\frac{0}{12.3}$	$\frac{0}{17.9}$	$\frac{0}{12.3}$	$\frac{0}{13.2}$	$\frac{0}{13.9}$	$\frac{0}{14.8}$	$\frac{0}{15.2}$	$\frac{0}{15.3}$	$\frac{0}{15.1}$	$\frac{0}{13.7}$	$\frac{0}{3.4}$
	$\frac{0}{\div 40}$	$\frac{0}{12.9}$	$\frac{0}{13.0}$	$\frac{0}{12.9}$	$\frac{0}{12.6}$	$\frac{0}{12.2}$	$\frac{0}{11.9}$	$\frac{0}{11.8}$	$\frac{0}{12.0}$	$\frac{0}{12.3}$	$\frac{0}{12.6}$	$\frac{0}{12.9}$	$\frac{0}{13.2}$	$\frac{0}{13.4}$	$\frac{0}{12.6}$	$\frac{0}{1.6}$
	$\frac{0}{\div 80}$	$\frac{0}{9.1}$	$\frac{0}{9.2}$	$\frac{0}{9.1}$	$\frac{0}{8.7}$	$\frac{0}{8.5}$	$\frac{0}{8.5}$	$\frac{0}{8.6}$	$\frac{0}{8.8}$	$\frac{0}{9.0}$	$\frac{0}{9.2}$	$\frac{0}{9.3}$	$\frac{0}{9.5}$	$\frac{0}{8.9}$	$\frac{0}{1.0}$	
	$\frac{0}{\div 120}$	$\frac{0}{4.6}$	$\frac{0}{4.6}$	$\frac{0}{4.6}$	$\frac{0}{4.5}$	$\frac{0}{4.5}$	$\frac{0}{4.6}$	$\frac{0}{4.6}$	$\frac{0}{4.7}$	$\frac{0}{4.7}$	$\frac{0}{4.7}$	$\frac{0}{4.8}$	$\frac{0}{4.9}$	$\frac{0}{4.6}$	$\frac{0}{0.4}$	

the day, on the other hand, insolation is greatest, and the temperature increases until, simultaneously with or some time after the maximum of insolation, it attains its maximum value. In the course of the afternoon, evening, and night, insolation decreases and with it the temperature until it again attains its minimum at sunrise the next morning. Deviations from these typical relations occur with irregular conditions of cloud-covering.

From the heated surface of the earth a current of heat now passes partly upward to the air, partly downward to the deeper-lying strata, and this current of heat is not arrested until the temperature at the surface of the earth has again dropped below that of the surroundings, at which juncture the current of heat begins to change its direction. The surface of the earth now receives heat from the lower strata and, though to a less extent, from the lower layers of the air. The result will then be that shown in table 32 1-2. The daily variation in temperature is greatest at the surface, thence it decreases upwards as well as downwards until it becomes practically zero, which value is attained at different depths, varying according to the heat-conducting power of the different kinds of soil.

Thus, it appears from table 32 that the daily variation in temperature penetrates far deeper into sandy soil than into snow. In snow the daily variation will as a rule be imperceptible at a depth of 10-20 cm., whereas in sandy soil it is not imperceptible until at a depth of c. 30-50 cm. This agrees well with the much smaller heat-conducting power of the snow. Other kinds of soil show still greater deviations, thus table 35 shows that granite rock has a considerably greater heat-conducting power, boggy soil on the other hand, considerably less heat-conducting power than loose sandy soil.

Another fact will appear from table 32, viz. the displacement of the moment of incidence of the maximum and the minimum at the various depths. While the temperature at the surface of the snow attains its maximum at 14 o'cl., this will not occur until 16-18 o'clock at 14 cm.s depth, and not until 24 o'clock at 24 cm.s depth. The temperature minimum varies in the same way.

The annual variation in temperature is as the daily variation. In the summer an unbroken current of heat will pass from the surface of the soil into the deeper-lying strata, in the winter the current will pass in the opposite direction. The annual amplitude will likewise decrease strongly with the distance from the surface, just as a displacement of the moment of incidence of the

maximum and minimum will take place at the different depths. Thus the temperature minimum in the lower strata will only occur simultaneously with the temperature maximum at the surface, and reversely.

The daily and annual mean temperature of the surface of the earth is higher than that of the air, just as the daily and annual amplitude is higher for the surface than for the air.

TABLE 33. **The annual Rise of Temperature**

in Soils with or without Vegetation or Snow Covering at Pawlowsk (Russia.) The figures give the mean values of a period of 5 years, 1891—95. After H. Wild 1897 p. 7.

	November	December	January	February	March	April	May	June	July	August	September	October	Years	Difference
Snow covering cm	3	16	31	46	49	19	»	»	»	»	»	»	(27)	»
Clouds	8.3	8.5	8.3	7.4	6.5	5.9	5.9	6.1	6.6	6.6	7.0	7.6	7.0	»
Air temperature C°	÷ 2.0	÷ 6.4	÷ 10.2	÷ 10.0	÷ 4.5	2.0	9.1	13.4	15.9	13.8	8.7	4.0	2.8	26.1
Natural external surface	÷ 2.5	÷ 6.8	÷ 10.3	÷ 10.3	÷ 6.1	2.0	12.3	17.4	19.4	15.7	9.2	3.5	3.6	29.8
Sandy surface 0 0 cm	÷ 2.6	÷ 6.6	÷ 10.4	÷ 9.6	÷ 3.5	4.3	12.3	16.7	18.9	15.5	9.0	3.6	4.0	29.2
÷ 40 »	0.9	÷ 2.6	÷ 6.1	÷ 6.4	÷ 2.4	1.8	8.3	13.3	16.7	15.2	9.8	5.4	4.4	23.1
÷ 80 »	3.3	0.7	÷ 1.9	÷ 2.7	÷ 1.2	0.2	4.9	10.1	14.1	13.9	10.3	6.9	4.9	16.7
÷ 160 »	5.7	3.8	2.2	1.2	0.8	0.8	2.4	6.2	10.0	11.3	10.3	8.2	5.2	10.
Vegetation or snow covered surface 0.0 cm	÷ 0.8	÷ 2.4	÷ 2.4	÷ 1.4	÷ 0.7	2.6	9.8	14.7	17.0	14.2	9.0	4.2	5.3	19.4
÷ 40 »	3.4	1.7	0.9	0.8	0.7	1.4	7.7	11.6	14.6	14.7	11.1	7.3	6.3	14.0
÷ 80 »	4.9	3.0	2.0	1.7	1.5	1.7	6.1	9.7	12.6	13.5	11.2	8.3	6.4	12.0
÷ 160 »	6.6	4.7	3.5	3.0	2.6	2.4	4.5	7.5	10.0	11.6	11.0	9.1	6.4	9.2

The facts described above apply to bare homogeneous sandy soil, as investigated by H. Wild at Pawlowsk, cf. table 33. If, on the other hand, the surface is clothed with a natural vegetation or covered with snow, a case likewise investigated by H. Wild in the same locality and shown in table 33, the facts will be otherwise. A bare sandy surface has a mean annual temperature of 4.0° with an annual amplitude of 29.2, a natural surface has a mean annual temperature of 3.6° and an annual amplitude of 29.2. The surface under snow and vegetation, on the other hand, has a mean annual

temperature of 5.3° and an annual amplitude of 19.4 . Thus, while a natural surface is on the whole similar to a bare sandy surface, the presence of a covering of vegetation or snow will cause a reduction of the annual amplitude of c. 10° and an increase of the mean annual temperature of no less than 1.30 .

This applies to the surface of the soil, but the deeper-lying strata too are affected by a covering of snow or vegetation, and in the same direction. There will be a decrease in the annual amplitude and an increase in the mean annual temperature. A comparison between the two sides of table 33 will show the numerical values.

A covering of vegetation will, in the summer, cause a lower average monthly temperature of the surface below it than the natural surface or a bare sandy surface would have done. This difference will, however, only amount to a couple of degrees. In the winter, however, a covering of snow will mean an immense increase of the surface temperature under the snow compared with that above the snow. According to Wild, a snow-covering of $30-45$ cm.s' depth will cause a temperature difference of $8-9^{\circ}$ between the surface of the soil and that of the snow. Thus a sandy surface has a January-February temperature of c. $\div 10^{\circ}$, while the surface below a snow-covering of $30-40$ cm. has only a January-February temperature of $\div 2^{\circ}$; at a depth of 40 cm the values are $\div 6^{\circ}$ and $+1^{\circ}$ respectively.

Very convincing and thorough investigations on temperature conditions in snow have been made by J. Keränen (1920). The investigations comprise two snow-periods 1915-16 and 1916-17, the temperature in the surface of the snow at various depths and at the surface of the soil being measured 3 times daily, at 7 o'clock, at 13, and at 21 o'clock. By means of these figures the average monthly temperature for the respective depths has been calculated. The mean values for the two periods have been given in table 34, where likewise the depth of the snow-covering is given, besides the temperature of the air, and the temperature at various distances from the surface for the year and for each month.

The snow-covering during the months November-April has an average depth of 47.8 cm and due to this an average surface temperature of $\div 14.2^{\circ}$ can only cause the temperature at the bottom, i. e. at the surface of the soil to drop to $\div 2.7^{\circ}$.

An investigation of temperature conditions in the snow in the various months will also show the varying isolation power of the

TABLE 34. Annual Variations in the Temperature

of the Air, Snow, and Soil in Sodankylä (Finland, $67^{\circ} 22' N.$, $26^{\circ} 39' E.$).

The investigations cover the period from November 1915 to October 1917 (cf. Keränen 1920, pp. 52—53).

	November—April	June—September	November	December	January	February	March	April	May	June	July	August	September	October	Average	Difference
Depth of snow cm	47.8	»	16.1	31.9	45.8	62.5	70.5	68.8	»	»	»	»	»	»	»	»
Precipitation mm	»	»	52.6	25.8	23.3	33.1	25.5	36.4	36.3	49.7	65.3	68.1	74.6	75.0	56.6	»
Clouds	»	»	8.2	7.9	8.1	7.7	6.3	7.9	7.8	6.9	7.0	8.0	7.1	8.8	7.6	»
Temperature of air C°	$\div 12.1$	10.6	$\div 8.2$	$\div 17.7$	$\div 14.0$	$\div 15.0$	$\div 13.6$	$\div 4.1$	1.2	11.9	14.4	11.7	4.5	$\div 1.2$	$\div 2.5$	»
Snow 0 cm.....	$\div 14.2$	»	$\div 9.6$	$\div 18.9$	$\div 16.1$	$\div 17.0$	$\div 15.1$	$\div 5.9$	*	»	»	»	»	»	»	»
$\div 10$ »	»	»	*	$\div 10.1$	$\div 10.2$	$\div 10.8$	$\div 10.4$	$\div 3.4$	*	»	»	»	»	»	»	»
$\div 20$ »	»	»	*	*	$\div 7.2$	$\div 8.2$	$\div 8.2$	$\div 3.0$	*	»	»	»	»	»	»	»
$\div 30$ »	»	»	*	*	$\div 4.9$	$\div 6.3$	$\div 6.6$	$\div 2.6$	*	»	»	»	»	»	»	»
$\div 40$ »	»	»	*	*	*	$\div 4.8$	$\div 5.4$	*	*	»	»	»	»	»	»	»
$\div 50$ »	»	»	*	*	*	$\div 3.7$	$\div 4.3$	*	*	»	»	»	»	»	»	»
$\div 60$ »	»	»	*	*	*	*	$\div 3.4$	*	*	»	»	»	»	»	»	»
Soil 0 cm	$\div 2.7$	13.2	$\div 2.8$	$\div 4.0$	$\div 3.3$	$\div 2.8$	$\div 2.7$	$\div 1.2$	1.9	15.3	18.3	14.0	5.1	$\div 0.5$	3.2	22.3
$\div 10$ »	$\div 1.9$	12.2	$\div 1.1$	$\div 2.5$	$\div 2.6$	$\div 2.1$	$\div 2.1$	$\div 1.0$	0.9	11.8	16.7	13.8	6.5	1.0	3.3	19.3
$\div 25$ »	$\div 1.4$	11.0	$\div 0.4$	$\div 1.7$	$\div 2.1$	$\div 1.7$	$\div 1.8$	$\div 1.0$	0.4	9.3	14.9	13.0	7.0	1.4	3.1	17.0
$\div 40$ »	$\div 1.1$	10.7	0.4	$\div 1.2$	$\div 1.8$	$\div 1.6$	$\div 1.6$	$\div 0.9$	0.2	7.9	14.3	13.1	7.7	2.2	3.2	16.1
$\div 80$ »	$\div 0.1$	9.0	1.3	0.6	$\div 0.2$	$\div 0.6$	$\div 1.0$	$\div 0.8$	$\div 0.2$	5.4	11.8	11.9	8.1	3.1	3.2	12.9
$\div 120$ »	0.8	7.2	2.4	1.3	0.6	0.3	0.1	$\div 0.1$	0.0	1.9	8.4	10.1	9.5	4.6	3.2	10.2
$\div 160$ »	1.1	6.6	2.7	1.7	0.9	0.6	0.3	0.1	0.1	1.5	7.0	9.4	8.4	4.9	3.1	9.3

snow. At the beginning of the winter when the snow lies lightly, a layer of a certain depth has a greater power of isolation than a layer of the same depth at the close of the winter, at which time the layer has grown more compact. Thus the table shows that the difference in temperature between corresponding layers is greatest at the beginning of a snow-period and decreases progressively until it attains its lowest value at the close of the winter. This fact has a certain practical significance in that the temperature at the surface of the soil will never be very much lower at the beginning of the winter than later on, in spite of the much slighter snow-covering at the beginning of the winter.

Investigations on the temperature conditions in soil with a different water content, of a different consistence, and with a different

TABLE 35. Average Maxima, Minima, and Amplitudes

of various Soils. After Homén, 1897, pp. 47–48. The investigations cover the period 10–13 August 1893.

	Granite			Sandy heath			Bog		
	Max.	Min.	Diff.	Max.	Min.	Diff.	Max.	Min.	Diff.
Air temperature C°...	22.7	9.6	13.1	»	»	»	»	»	»
Vegetable covering ...	32.5	12.6	19.9	37.7	6.4	31.3	32.8	2.2	30.7
0 cm	34.8	14.5	20.3	42.3	7.8	34.6	27.7	6.3	21.4
1 »	33.1	15.2	17.9	35.9	9.7	26.2	23.9	8.9	15.3
2 »	31.9	15.8	16.1	30.6	11.3	19.3	20.6	11.1	9.6
5 »	30.4	16.6	13.8	24.7	12.8	11.8	16.7	13.9	2.8
10 »	28.9	17.2	11.7	22.2	14.4	7.8	16.2	14.8	1.5
20 »	26.1	18.2	7.9	19.4	15.5	3.9	15.3	14.9	0.4
30 »	24.3	19.1	5.2	17.7	15.9	1.8	14.3	14.2	0.1
40 »	22.9	19.5	3.4	16.2	15.5	0.7	13.5	13.4	0.05
50 »	21.7	19.6	2.1	15.0	14.8	0.3	12.4	12.4	»
60 »	20.9	19.6	1.4	14.2	14.1	0.1	11.7	11.6	»

clothing of vegetation have been made in Finland by Th. Homén and described in a series of works (1894, 1896, and 1897). Tables 35, 36, and 37 give the chief data of these works. Table 35 comprises the daily heat maximum, heat minimum, and amplitude for granite, sandy soil, and boggy soil, respectively a solid, a loose, and a damp rock. The figures are the mean values of a series of investigations. Table 36 shows the daily amplitude for various kinds of soil, sandy soil, clayey soil, and boggy soil with or without wood or a covering of cultivated plants (cereals). Table 37 shows the annual mean temperature, the annual variation in temperature, i. e. the difference between the mean temperatures of the coldest and warmest months and the mean temperature of each month at different depths in soils with a different clothing of vegetation, thus at 0.5, 1.0, and 2.0 m for open grassfield, birchwood, and firwood.

A comparison between the temperature conditions of solid rock and loose sandy soil shows a much greater current of heat in the solid than in the loose soil. Taking the average of 4 days, the surface of a granite rock will be heated to 34.8° by day. The heat accumulated at the surface will comparatively rapidly spread downwards so as to make the temperature maximum at a depth of 60 cm no less than 20.9; for sandy soil the same figures are respectively

42.3 and 14.2. A comparison between the daily temperature amplitudes for rock and sandy soil shows, for the same depths, apart from the uppermost layers, a greater amplitude for the solid than for the loose soil. All these figures show that sandy soil is a better isolator than rocky soil.

TABLE 36. Average Diurnal Variation of Temperature

in different Soils with differing Vegetation. After Th. Homén.

Nos. 1—3 (1897, p. 48); 4—14 (1894, p. 231).

	Granite	Sandy heath	Bog	Sunny open heath		Forest-clad heath	
	10—13°/s 1893	10—13°/s 1893	10—13°/s 1893	12—13°/s 1892	6—8°/s 1892	12—13°/s 1892	6—8°/s 1892
	1	2	3	4	5	6	7
0 cm depth..	20.2°	34.6°	21.4°	18.4°	22.0°	7.1°	6.3°
2 » » ..	16.1	19.3	9.6	13.0	13.2	4.3	3.6
5 » » ..	13.8	11.8	2.8	9.4	9.2	2.7	2.1
10 » » ..	11.7	7.8	1.5	6.4	6.2	1.5	1.3
20 » » ..	7.9	3.9	0.4	2.9	2.7	0.7	0.6
40 » » ..	3.4	0.7	0.05	0.6	0.4	0.2	0.1
	Sunny open bog		Forest-clad moor		Boggy field		Clayey field
	12—13°/s 1892	6—8°/s 1892	12—13°/s 1892	6—8°/s 1892	preserv. 12—13°/s 1892	harvest. 6—8°/s 1892	12—13°/s 1892
	8	9	10	11	12	13	14
0 cm depth..	18.1°	14.7°	8.2°	7.4°	12.0°	18.6°	8.5°
2 » » ..	11.1	9.5	4.8	4.1	7.4	9.9	6.9
5 » » ..	4.4	3.9	1.9	1.7	3.6	4.7	4.0
10 » » ..	2.1	1.8	0.8	0.7	1.1	1.2	2.4
20 » » ..	0.5	0.5	0.2	0.2	0.3	0.3	1.0
40 » » ..	0.04	0.04	0.02	0.02	0.03	0.03	0.3

If, next, the dry soil, the sandy heath, is compared with the damp soil, the bog, the above-mentioned deviations are seen to be continual. The surface of the bog only attains a temperature maximum of 27.7°, owing to a great deal of heat becoming latent by evaporation of the water present in the bog. At a depth of 60 cm the maximum temperature is only 11.70. The minimum temperature of the surface is no less than 6.3° and is thus the lowest of the temperatures

of the three types of soil. Very striking is the daily variation in temperature, this is not only rather small at the surface, but already at very slight depths it is practically nil.

Table 36 shows the average daily variation in temperature for sandy soil, clayey soil, and boggy soil, with or without a covering of vegetation i. e. of cornfield or wood. These investigations show the same conditions as table 35, viz. that sandy soil has a greater daily variation of temperature than boggy soil at the same depth, and that the daily variation in temperature penetrates to greater depths in sandy than in boggy soil. If the soil is covered with vegetation, i. e. wood or cornfields, the result will be in the first place a decrease in the daily variation of temperature.

TABLE 37. Annual Variation of Temperature

in Soils with different Vegetable Covering in Heinäis, Finland.
After Th. Homén 1896, p. 147.

	January	February	March	April	May	June	July	August	September	October	November	December	Year	Difference	
Firwood 0.50 m	1.6°	1.2	1.0	1.1	4.1	10.4	12.6	12.8	10.7	6.5	3.7	2.1	5.7	11.8	
	1.00 >	2.3	1.8	1.4	1.3	2.9	7.5	10.0	11.0	10.0	7.3	4.7	3.1	5.3	9.7
	2.00 >	3.6	2.9	2.4	2.2	2.6	4.7	7.0	8.5	8.7	7.7	5.8	4.3	5.0	6.5
Birchwood 0.50 m	1.0°	0.4	-0.2	0.3	2.3	7.5	10.2	10.9	9.4	5.6	3.0	1.6	4.3	11.1	
	1.00 >	2.0	1.5	1.0	0.8	1.8	4.9	3.4	8.7	8.4	6.3	4.3	2.9	4.2	7.9
	2.00 >	3.5	2.9	2.6	2.2	2.3	3.9	5.7	7.0	7.5	6.8	5.6	4.4	4.5	5.3
Grassfield 0.50 m	1.1°	0.6	0.3	0.4	1.0	4.6	8.5	9.8	8.7	5.6	3.3	1.6	3.8	9.5	
	1.00 >	2.0	1.4	1.0	0.9	1.1	3.3	6.5	8.1	7.9	6.1	4.2	2.7	3.8	7.2
	2.00 >	3.1	2.4	2.0	1.7	1.6	2.3	4.3	5.8	6.4	5.9	4.9	3.8	3.7	4.8

A similar series of investigations on annual variations in temperature and temperature conditions is only found respectively for sunny open and wooded sandy soil, but unfortunately not for damp soil, whether such as is constantly damp throughout the year, or such as is damp in winter but dry in summer. Table 37 (after Homén 1896) shows the annual mean temperature at various depths for respectively sunny open and wooded soil, the mean temperature of each month and the difference between the lowest and highest

monthly mean temperatures. The table confirms the rule previously laid down that the amplitude decreases with the distance from the surface, and further that it is greatest for the sunny open soil, less for the wooded soil. This applies in still greater degree to the mean temperature of the warmest month and to the annual mean temperature. The sequence is as follows: grassfield → birchwood → firwood.

From a knowledge of the daily and annual variations in temperature it is possible to determine the heat-conducting power of a rock, this quantity being the less the slower the maximum and minimum spread in the soil, or the quicker the amplitude decreases downwards.

After Hann (1926, p. 800) we give the following values for a series of natural rocks (minute, cm.).

Sandstone	1.39
Clay with an admixture of sand	0.82
Sandy soil.....	0.52
Finnish granite	1.14
Heath.....	0.32
Boggy soil.....	0.13
Loose snow	0.16
Compact snow.....	0.24
Ice	0.68
Frozen earth	0.56
Earth not frozen.....	0.32

However, the heat-conducting power is not only different for the different rocks, it also varies in the same rock according to the air and water-content. The more solid and moist a rock is, the better is its heat-conducting power.

SUMMARY.

1. By investigations on the quantitative distribution of the life-forms in the floras, from temperate to progressively arctic regions, Raunkiær has shown that the chamaephyte percentage is subject to a steady increase from southern towards northern regions. Current conditions in the surrounding seas show an appreciable influence on the course of the individual Ch biochores, a warm northgoing current causing a decrease of the Ch percentage, while a cold south-going current causes an increase of the Ch percentage. This appears plainly from conditions along the coasts of Greenland and Iceland.

2. If the Icelandic flora is divided into groups according to the northern and southern limits of the species, 7 species groups will result, distributed in 2 main groups. The 2 main groups represent species with respectively a northern and a southern distribution. The sub-groups within each main group differ from each other with respect to their northern limit. If the biological spectra of the individual groups are examined, a continued increase of the Ch percentage from the species group with the most southerly distribution to that with the most northerly distribution will be observed. If likewise the variation of the biological spectra and the species group spectra in the flora lists of the separate parts of the country and altitudinal zones is examined, the variation is the same in both cases, but greatest in the case of the species groups. Species groups and life-forms may thus be regarded as indicators of environment and may be made the basis of considerations on external factors where these are unknown.

3. Iceland's Ch percentage ranges it among the boreal hemicyclopedia-chamaephyte climates, the Ch percentage for the whole country being 15.2. The 20 p. c. Ch biochore for the country as a whole lies at a level of c. 300 m above the sea. Between this line and the snow-line, which lies at a level of c. 1200 m, it is possible

to distinguish between a series of zones, a lower and an upper highland zone, and a nival zone.

The lines between these zones can be drawn approximately as follows. The lower highland zone extends from the 300 m curve to the 600 m curve and has a Ch percentage of from 20 to 25; the upper highland zone extends from the 600 m curve to the 800 m curve and at its upper limit has a Ch percentage of 40; the nival zone is the zone between the 800 m curve and the snow-line; it has a Ch percentage of 40—50. Even though the position of the limits of the zones must be taken with some reservation, they agree well with conditions in the adjacent countries. Thus in Scotland the 20 p. c. Ch biochore lies at c. 800 m above sea-level, in the Faeroes at c. 500 m, in Greenland the 20 p. c. Ch biochore lies at the level of the sea in 60—61° N.

4. An investigation of the peculiarities of the flora in the separate parts of the country and the altitudinal zones shows that the differences are especially due to differences in temperature. The differences in the vegetation are likewise due to this factor.

The temperature of the soil differs according to the degree of snow-covering and water-covering, though in different ways. In the winter the geiri vegetation with its constant snow-covering as well as the flói vegetation with its constant water-covering are protected from the frost. Hence the result in both cases is a vegetation consisting principally of southern species, even though the two areas have not one species in common, while the snow-bare vegetation, mellar and mosathembur, which is most exposed to the cold of winter, consists principally of arctic species, and the intermediate areas, mo, jaðar, and myri, both as regards environment and biological conditions, occupy an intermediate position.

In the summer the flói vegetation has a constant covering of water, the specific heat and evaporating heat of which does not allow of so high a degree of heating as an equal amount of heat produces in the geiri vegetation. The result is, then, that a series of the most heat-loving species do not occur on water-covered soil, but only in the geiri. Soil with a constant water-covering is warm in winter, but cold in summer. The soil with a constant snow-covering in the winter is warm both summer and winter; both these circumstances are strikingly manifested in the composition of the vegetation.

The sequence dry, moderately moist, and moist soil, or mo,

jaðar, and myri, handsomely illustrates the influence of the degree of moisture on the temperature of the surface. — The snow-covering is the same for the three types of vegetation, viz. the normal snow-covering of the country.

In winter the dry soil is exposed to the hardest frost, while the moderately moist and especially the moist soil are protected by the moisture of the earth. In the summer, the moist soil cannot, on account of its water content, attain as high a temperature as the dry and moderately moist soils. The last-mentioned is dry in summer, like the mo.

Since the moderately moist soil has the advantages of moist soil in the winter, and of dry soil in the summer, it must be the most favourable of these three types for southern plants. This will be confirmed by an examination of table 38.

Between dry and moist soils there is a peculiar difference. The dry soil, the mo, is relatively cold in winter but dry in summer, while the moist soil, the myri, is relatively warm in winter and cold in summer. And, as a matter of fact, the result is that the mo has more high-arctic species requiring a low temperature and more species requiring higher temperature than the myri. Conditions in still moister and still drier vegetations than myri and mo, respectively, further confirm this difference.

The halla myri is another case in point. Owing to the constant supply of ground-water this myri becomes still warmer in winter and still colder in summer than the usual type, the fór myri. And the result is a further reduction of the number of species requiring cold and, since the winter lasts longer than the summer, an increase of the species requiring warmth. The effect of the cold water in the summer on the composition of the vegetation is likewise appreciable.

Since in Iceland it is the temperature in winter and in Denmark the temperature in summer which determines the formation of the types of vegetation, the halla myri vegetations of the two countries form a peculiar contrast. In Denmark the halla myri is characterised by its high content of arctic plants, but in Iceland by its high content of southern plants. Even in Iceland, however, the cold water in the summer tends to give the vegetation an artic character.

Around the hot springs the vegetation consists exclusively of the species requiring most heat.

TABLE 38.

Species-group spectra and biological spectra of the different types of
Vegetation on Iceland, based upon statistical investigations.

	Number of Localities examined	Points-sum	Number of species	Density of species	A	E	A 3	A 2	A 1	E 4	E 3	E 2	E 1	Ch	H	G	HH	Th
Mosathembur	11	2568	9	2.3	83	17	70	13	1	14	1	4	»	27	40	33	»	»
Melar	16	10658	24	6.8	72	28	48	18	6	24	4	0.5	0.1	47	41	11	»	2
Mo	34	43908	33	13.3	53	47	30	15	9	27	10	9	0.5	31	52	16	»	0.5
Jaðar	8	10140	39	13.2	47	53	23	14	10	31	12	10	0.1	18	53	28	1	1
Formýri	18	15240	26	9.4	49	51	22	18	9	38	12	1	»	24	21	49	5	0.2
Hallamýri.....	5	4180	25	8.3	44	56	17	22	5	25	21	11	»	8	28	58	6	1
Flöi.....	9	1740	4	1.9	28	72	5	3	20	37	36	»	»	2	13	76	10	»
Geiri	15	15374	27	11.0	37	63	23	10	4	24	26	13	1.1	34	50	16	»	0.1
Forest undergrowth	6	5592	33	8.6	28	72	14	10	4	22	37	11	3	12	72	16	»	»
Subularia flag.....	2	404	5	2.0	14	86	14	»	»	21	65	»	»	»	11	18	»	71
Flag.....	5	4852	25	9.9	58	42	38	19	»	15	25	1.4	0.1	13	60	12	»	15
Valllendi	6	4092	18	6.9	25	75	16	0.3	9	20	18	36	2	13	67	20	»	1

5. The low temperature in winter being the factor which has the greatest bearing on the vegetation, a natural system of the Icelandic types of vegetation, i. e. a system in which the factors are given in the order of their degree of importance for the vegetation, must give as the first principle of division the conditions of snow-covering, as the next, the conditions of moisture, and so forth.

Hence, the types of vegetation investigated in this treatise must be ranged in the following order.

I. Vegetation bare of snow.

1. Soil covered with moss

Mosathembur (moss heath, Grimmia heath)

2. Soil covered with gravel

Melar (fell field)

II. Vegetation with normal snow-covering.

1. Soil dry

Mo

2. Soil moderately moist

Valllendi

- a. Soil covered with vegetation, level
- b. Soil covered with vegetation, knolly
- c. Soil bare, with smallknolls

Jaðar (grass mo)
Flag (clayey flats)

3. Soil moist	Mýri
a. Stagnant water	Fór mýri (swampy mýri)
b. Running water	Fét mýri
c. Springs	Halla mýri
4. Soil always covered with water	
a. Stagnant water	Flói
b. Running water	Fén
c. Springs	Dý

III. Vegetation with a constant and deep snow-covering

1. Normal light conditions, no leaf-fall Geiri (snow patch)
2. Shade and leaf-fall Forest ground

6. Of the individual types of vegetation the following may be mentioned.

The mosathembur vegetation is bare of snow in the winter. The surface is covered with a dense and thick carpet of moss in which there occurs a scattered vegetation of high arctic plants poor in species. The amount of geophytes is unusually large. As a climatically conditioned type the mosathembur vegetation is confined to the North Atlantic region, in Iceland to the higher levels of South Iceland and especially East Iceland.

The mellar vegetation is likewise bare of snow in the winter. The surface is covered with gravel and is dry, with polygonal formation or solifluction. The vegetation is open, but with a relatively high number of species and density.

The mo vegetation, in point of environment, is characterised by a normal snow-covering and by the fact that it is unaffected by the ground water. The surface is knolly and covered with vegetation. The vegetation is both rich in species and dense, and consists of an equal mixture of arctic and southern plants which are either Ch or hemicryptophytes.

The jaðar vegetation like the mo has a normal snow-covering but is confined to moderately moist soils, i. e. soils dry in summer and wet in winter. The surface has large knolls and is covered with a dense vegetation rich in species (both the number and density of species attain their maximum in jaðar). The vegetation consists of an equal mixture of arctic and southern species, though compared with the adjacent types the southern species attain a relative maximum here. H are the dominant life-form, attaining their

maximum development in jaðar. Ch are of slight importance, while the number of G is on the increase.

The valllendi vegetation is a variant developed on the cones deposited by the streamlets of melting snow. There is no knoll formation and the vegetation is that of a more southern environment.

The flag vegetation. The surface is a bare clayey flat with scattered knolls and stones. The vegetation is characterised by its high therophyte percentage, though in jaðar, too, Th attain a relative though small maximum. Arctic species are more dominant in flag than in jaðar or especially valllendi. The jaðar vegetation seems to be confined to the Icelandic lowlands, to the jaðar or the transition from mo to myri.

The myri vegetation is peculiar to moist soil which must not, however, be covered with water all the year round. The surface is knolly. Here the vegetation likewise consists of an equal mixture of arctic and southern plants, but the most arctic and the most southerly either do not occur or their number is much reduced compared with that of mo and jaðar. G are the dominant life-form, Ch attain a relative maximum, while the number of H is much diminished. The number and density of the species are appreciably less than in mo and jaðar.

The types of myri occurring in Iceland are as follows.

Fór myri, which develops in depressions with stagnant water.

Halla myri, which develops in places where the ground water comes to the surface, thus especially at the foot of mountains.

Fét myri, which occurs near running water, along the banks of rivers, near the sea etc.

The flói vegetation develops where the soil is constantly covered with water all the year round. The surface is level, without knolls. The vegetation is very scattered and poor in species and consists almost exclusively of southern plants. The dominant life-form is G. The hydrophytes or helophytes likewise attain their maximum development in the flói.

The geiri vegetation is confined to soil with a constant and deep snow-covering from early autumn to late spring. The surface is always level, without knolls. The vegetation consists principally of southern plants, notably those requiring the highest temperature which are found in greatest quantity here. The dominant life-form is H, of less importance are Ch and especially G. Both the number and density of species are relatively high, though less than in the mo.

The forest ground vegetation resembles the geiri vegetation in external factors and in its main features. The density, the number of high-arctic plants, and the quantity of Ch are less in forest ground than in geiri, while the quantity of H is higher. The cause for this may perhaps be found in the differing illumination and the more constant protection from frost in the forest ground than in the geiri.

Each of the types of vegetation discussed above comprises a great number of formations which have not, as yet, been more closely examined.

7. Our knowledge of the quantitative distribution of the individual types of vegetation in the various parts and altitudinal zones of Iceland is as yet rather deficient. Of the percentage of types in the individual altitudinal zones, the following particulars may be given.

I. In the lowlands, below the 20 p. c. Ch biochore, the 300 m curve, the dominant features of the landscape are forest, mó (especially heather mó), jaðar, littoral meadow, flag, myri (*fór myri*, *halla myri*, and *fét myri*), flói, dý and fén, and lowland melar.

II. In the lower highland zone, 300—600 m above sea-level, the types of vegetation are melar (highland melar), mosathembur, mó (level and knolly), jaðar, myri (*fór myri*), flói, dý, and geiri (including the *Salix herbacea* and the *Sibbaldia* vegetation).

III. In the upper highland zone the vegetation is either melar or geiri (especially *Anthelia* crusts).

IV. In the zone between the 800 and 1200 m curves, the nival zone, a very scattered melar vegetation is recorded. The larger or smaller accumulations of snow are another feature of the landscape. Above the 1200 m curve, the snow line, we come to the

V. zone, the jökulls, where all higher vegetation is excluded on account of the continuous snow-covering.

The forces that go to form the various types of vegetation are, in the lowlands, especially the differences in moisture, in the highlands, the differences in snow-covering.

8. The investigation of the distribution of species, species-groups, and life-forms in the formations according to increasing prevalence of one and the same external factor has brought to light the following facts.

In a given scale of one and the same external factor the individual species attain maximum frequency, i. e. minimum distance between individuals, at some point in the scale. Passing from this point towards either greater or less prevalence of the factor under

consideration, the frequency of the species gradually decreases, i. e. the distance between individuals grows greater and greater and at last the species entirely disappears. This applies to all species. The individual species may be distinguished with respect to the position of the maximum in the scale, the magnitude of the maximum, and the number of degrees in the scale which the species covers.

The proportional distribution of the species in a given scale has proved the same wherever it has been more closely investigated.

The distribution of Raunkiær's life-forms in the scale of external factors is the same as that of the individual species. The sequence of the maxima of the life-forms in the scale of moisture from the most moist to the driest section is as follows: HH→G→H→Ch→(Th). This sequence occurs wherever conditions have been closely examined and remains the same whether the succession is determined by means of the number of individuals (frequency sum) or the number of species.

In the scale of snow-covering, Ch occur in greatest quantity in the "sections devoid of snow", H in the opposite sections. These conditions are repeated wherever the facts have been investigated, and remain the same whether calculated by means of the number of individuals or by means of the number of species.

The distribution of the species groups in the scales of external factors would seem to open up new possibilities of determining the factors which are active in the distribution of plants.

Fig. 1 is to be found on page 21, the others are printed on
plates I—XII.

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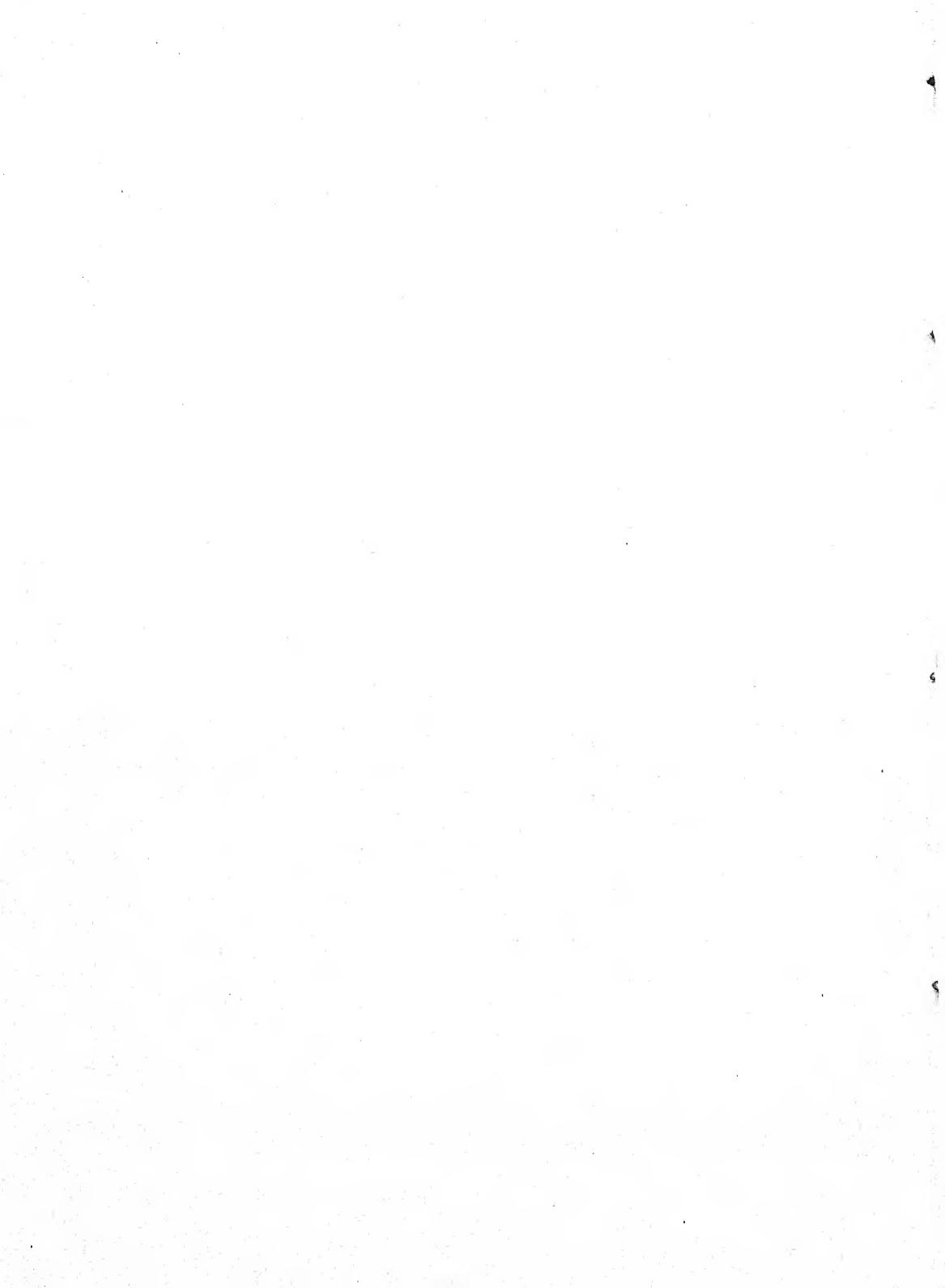
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PLATES I-XII



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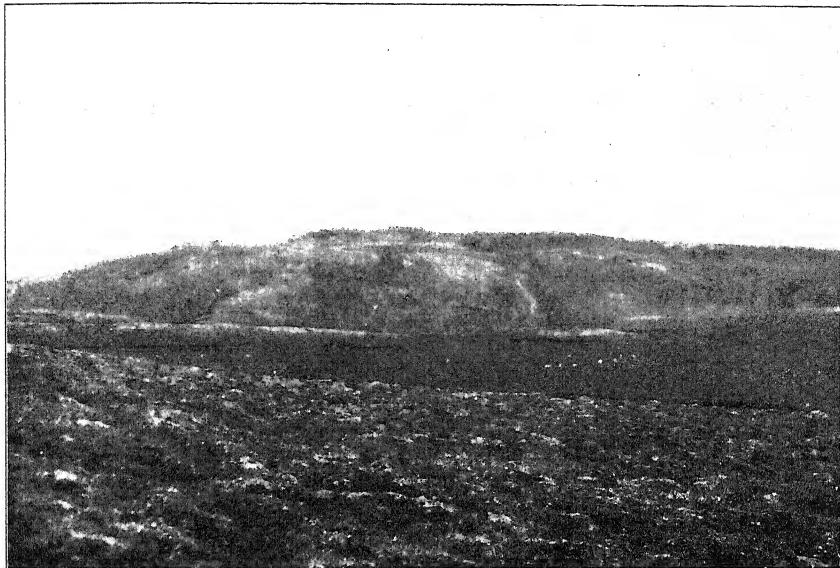


Fig. 2. Lýngdalur with Hrólfsdalur.

In the foreground mo vegetation, further back some narrow strips of mo with mosathembur (the lighter areas). In the background Hrólfsdalur with alternating areas of melar and mo. In the depression in centre, a myrl.

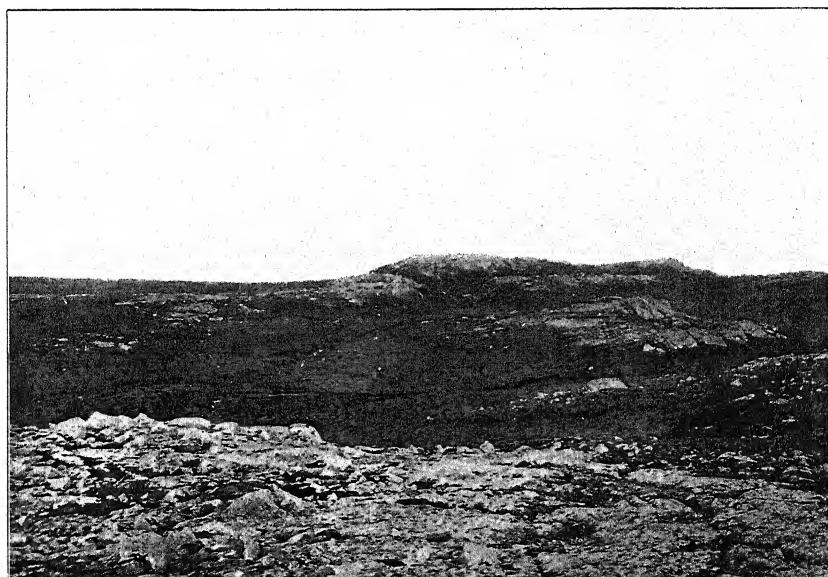
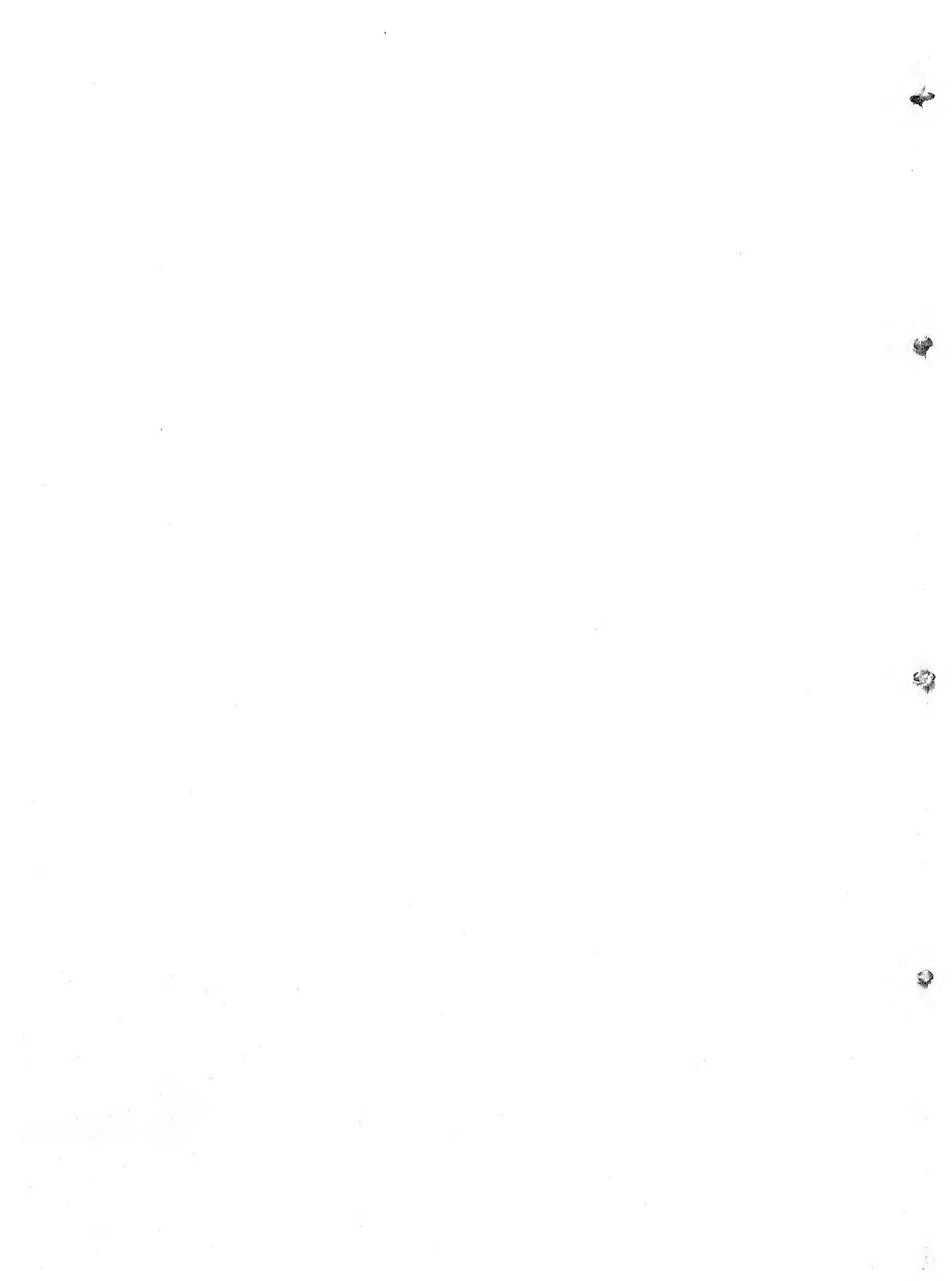


Fig. 3. Thrasaborgir.

The light areas in the foreground are mosathembur, in centre, a large patch of snow, geiri, with level surface. The knolly parts between geiri and mosathembur are mo. The picture is taken from the south, looking due north.



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Fig. 4. The Mosathembur Vegetation on Lýngdalsheiði.

The thick carpet of moss is intersected by long narrow fissures with a special vegetation.
The composition of the vegetation is shown in table 9 A, p. 40.



Fig. 5. The Melar Vegetation on Lýngdalsheiði.

The bottom is covered with gravel containing scattered stones. In the background Kalfstindar.
The composition of the vegetation is shown in table 10 A, p. 44.



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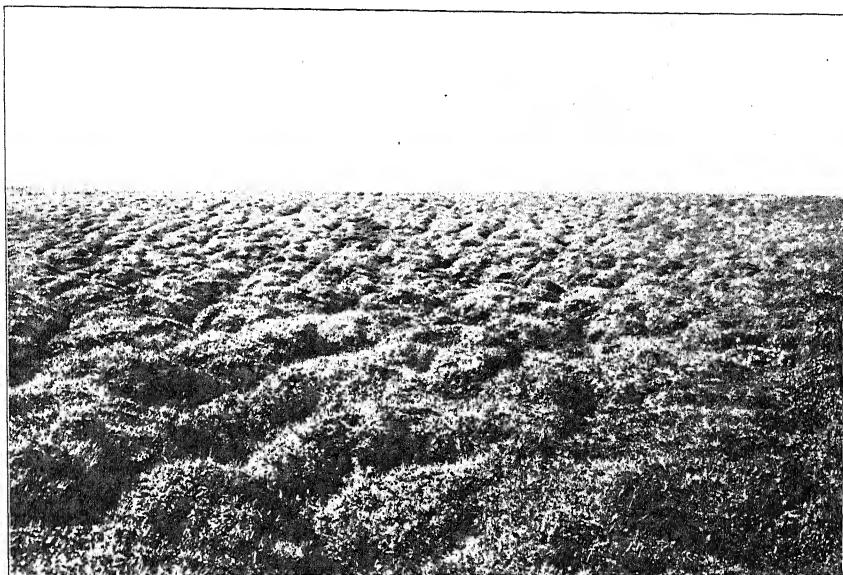


Fig. 6. The Mo on Lýngdalsheiði.

The ground with pronounced knolls. For vegetation, see table 11 A, pp. 48—49.

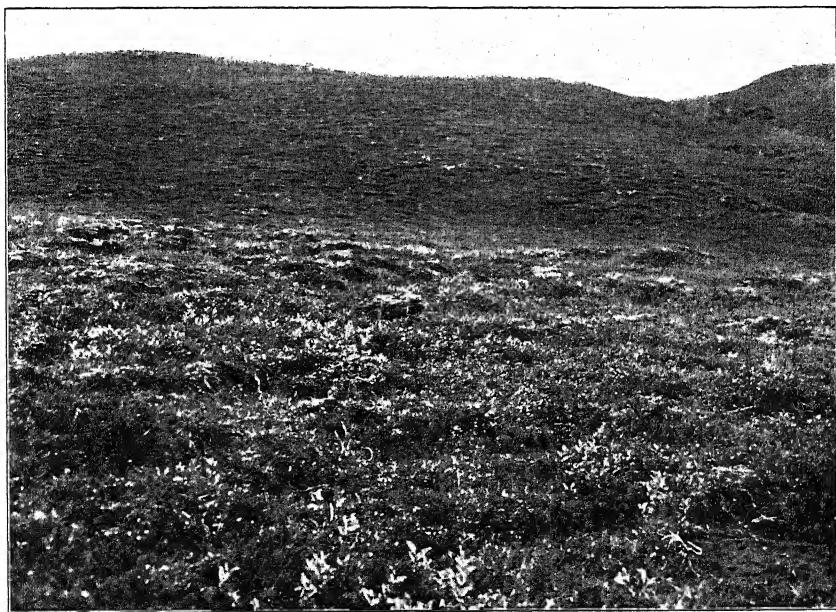
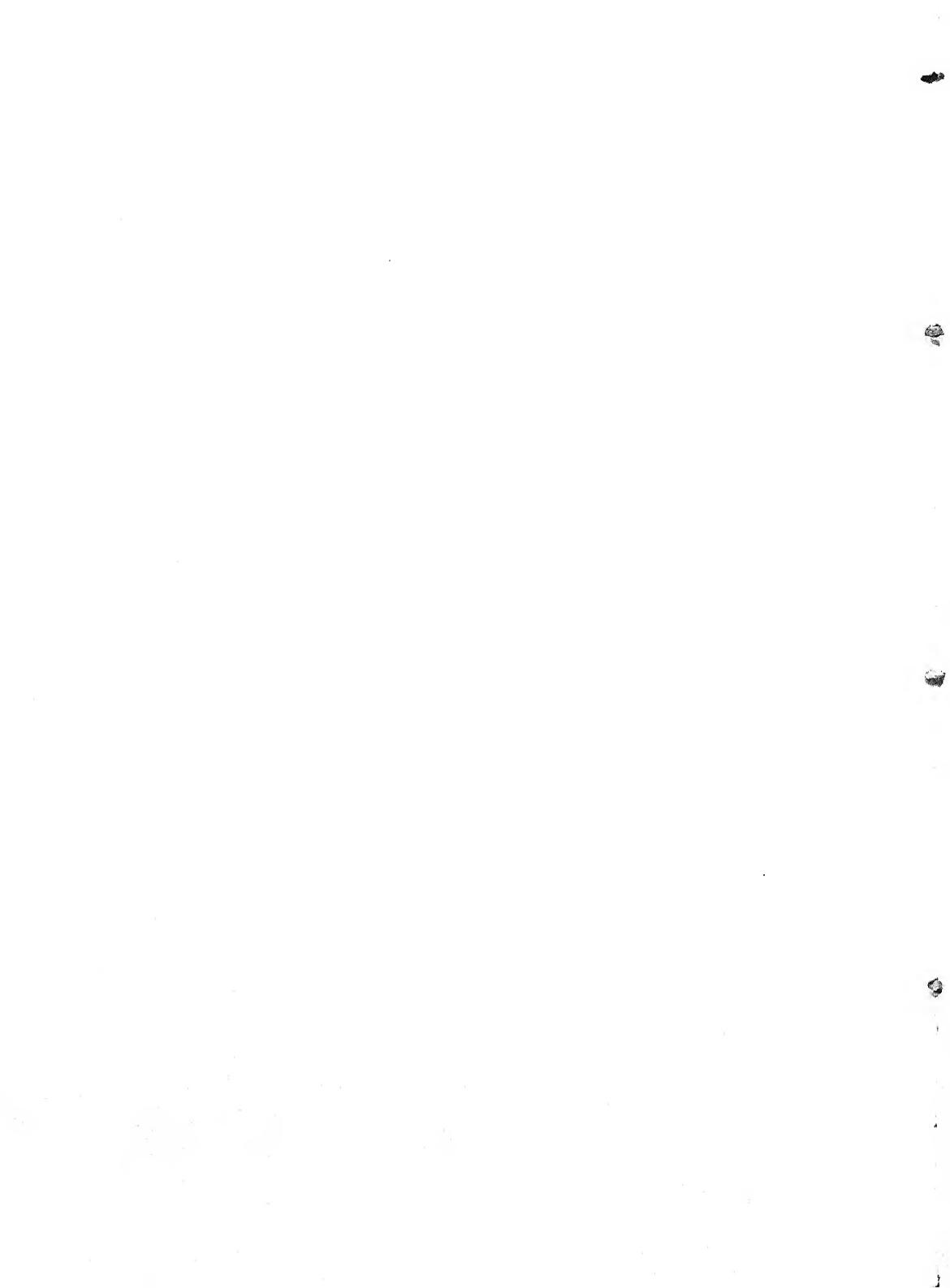


Fig. 7. Mo on the western Side of Lýngdalur.

The knolls on the slope are different from (more elongated than) the knolls on level ground.



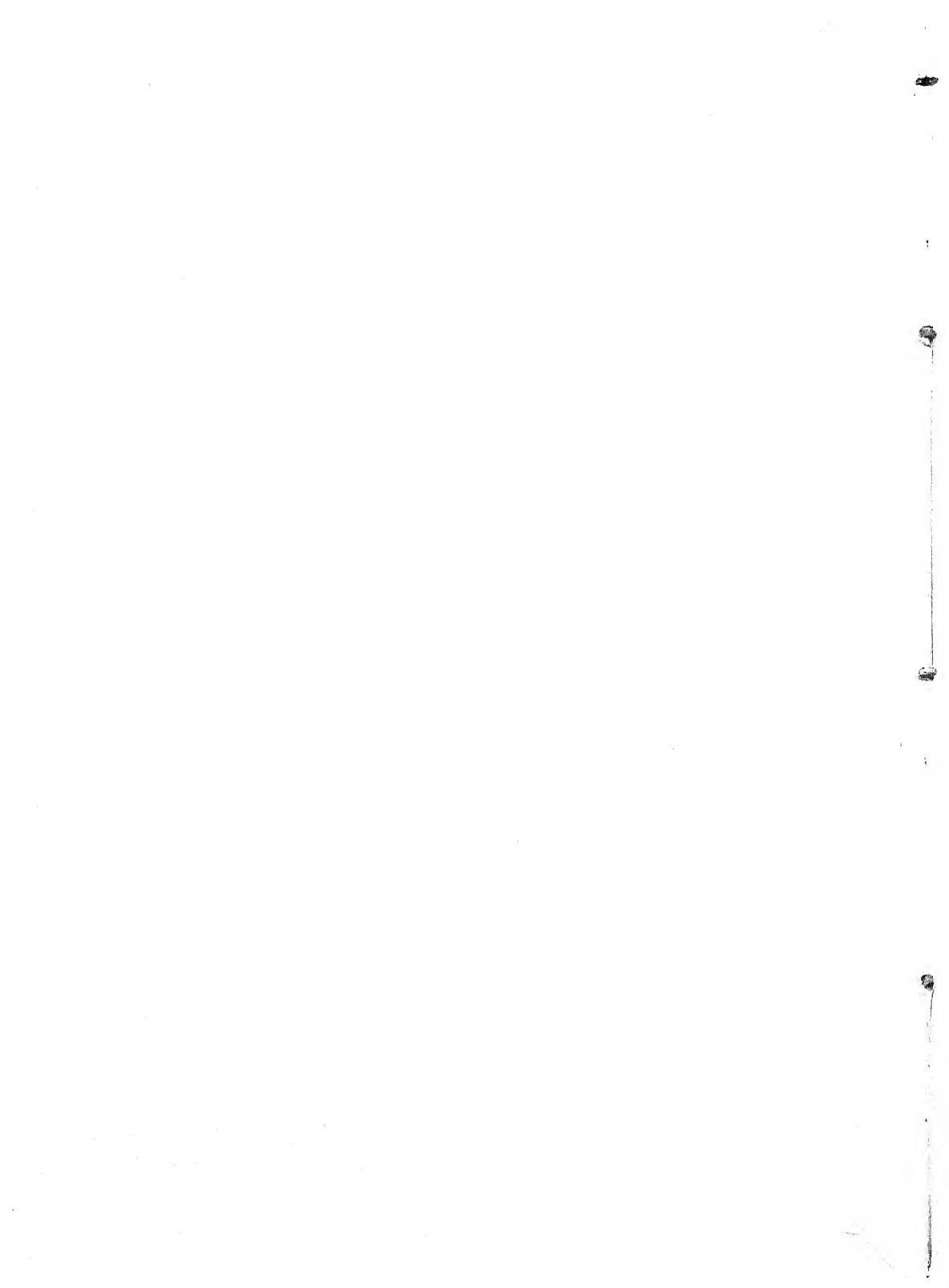
THE BOTANY OF ICELAND. VOL. III (H. MØLHOLM HANSEN)



Fig. 8. The Vallendi Vegetation on Lýngdalsheiði.
Surface level, without knolls. For vegetation see table 12 A, p. 52.



Fig. 9. Patch of Snow from the western Side of Lýngdalur.
The surface of the snow patch is level in contrast to the knolly surface of the surrounding moor.
For vegetation see table 13 A, pp. 56—57.



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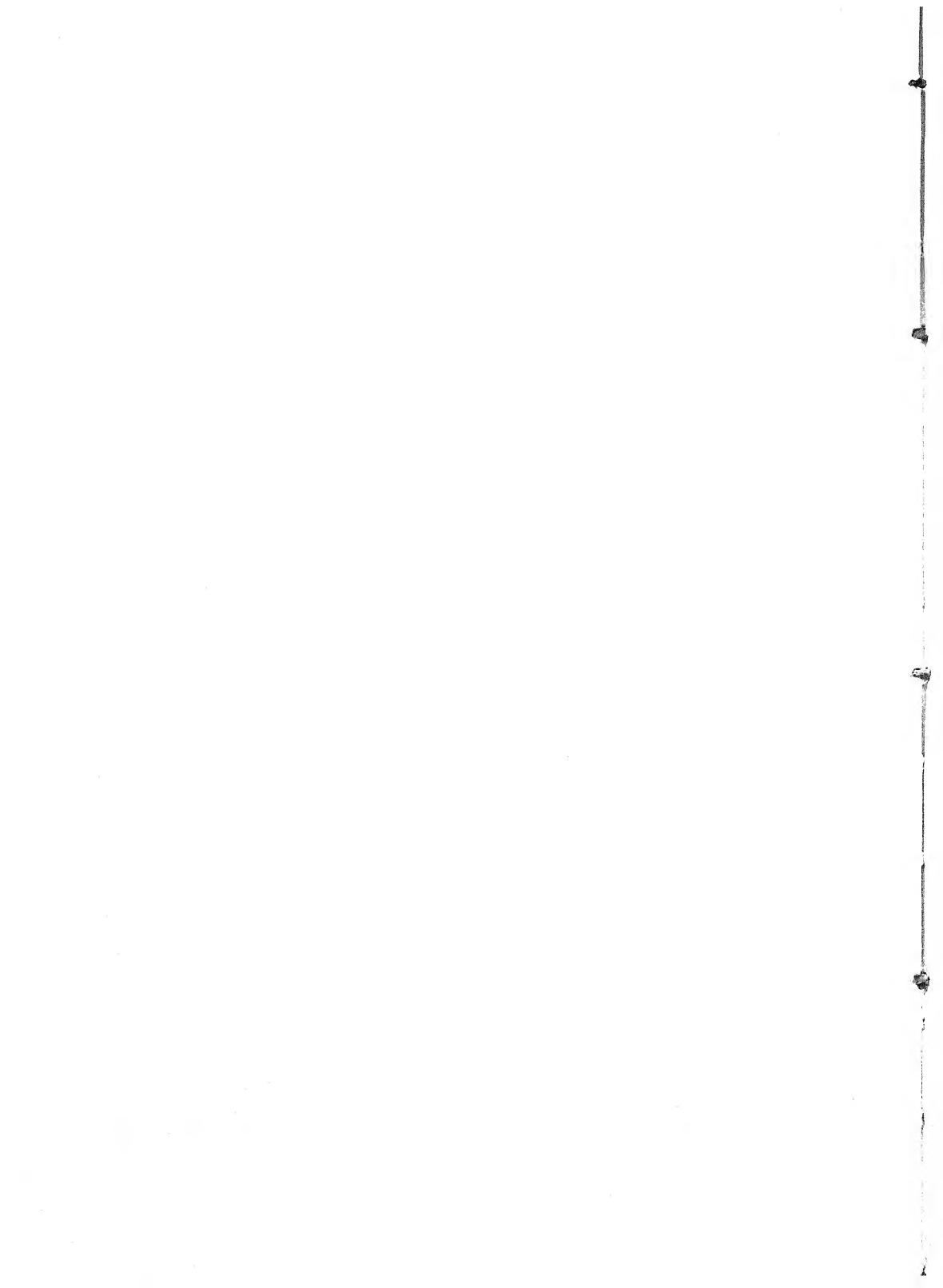
Fig. 10. Patch of Snow on Lýngdalsheiði.

Altitude c. 300 m. The picture shows the snow patch distinctly marked off from the surrounding mo.



Fig. 11. Mýri at Björk.

Surface knolly. For vegetation see table 15 A, pp. 66—67.
In the background Lýngdalsheiði and the Björk Farm.



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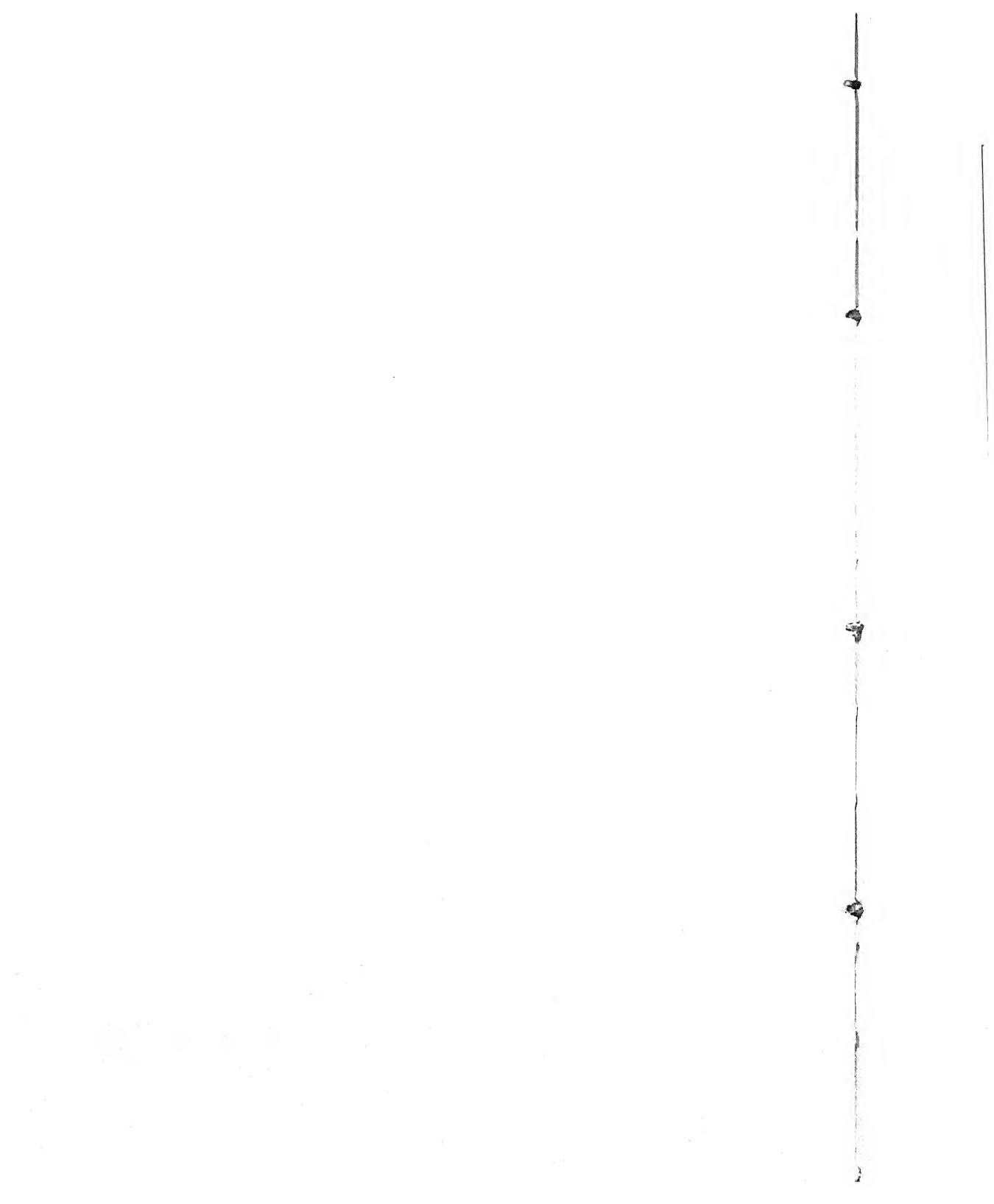
Fig. 12. Flag Mo at Lækjamót.

The picture shows the surface of the flag mo covered with small knolls in contrast to the larger knolls of the mo (left), and the sharp line of demarcation between flag and myri (right). For the composition of the vegetation see table 17 A, pp. 72—73.



Fig. 13. A smaller Section of fig. 12.

The surface features, the bare clayey ground with small grass knolls and stones, are more distinct.



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Fig. 14. Forest Glade at Norðtunga.

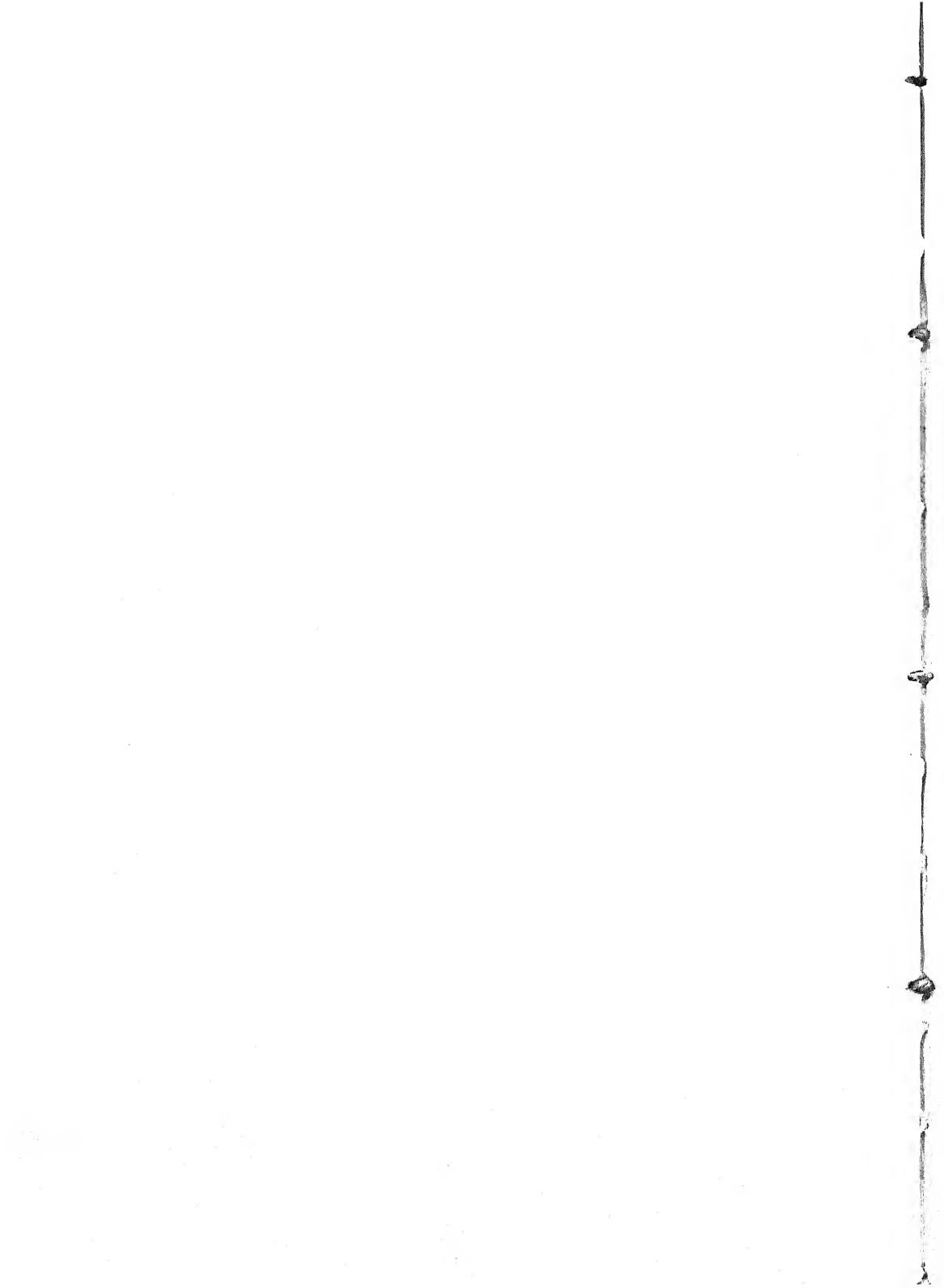
For the composition of the vegetation see table 21 A, pp. 90—91.



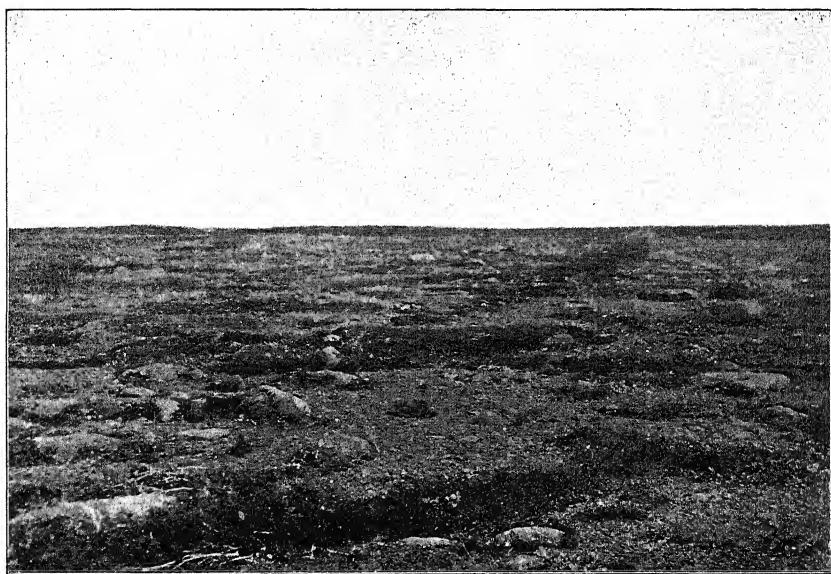
Fig. 15. Melar from the Crest of a Hill on Arnarvatnsheiði.

The surface covered with larger or smaller stones without solifluction curves.

For vegetation see table 22 A, 1—6, pp. 104—105.



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Figs. 16—17. Melar from a Slope,

viewed from above (fig. 16) and from below (fig. 17). The solifluction curves are much more conspicuous in the latter than in the former view. Vegetation practically the same as above, see table 22 A, 1—6, pp. 104—105.



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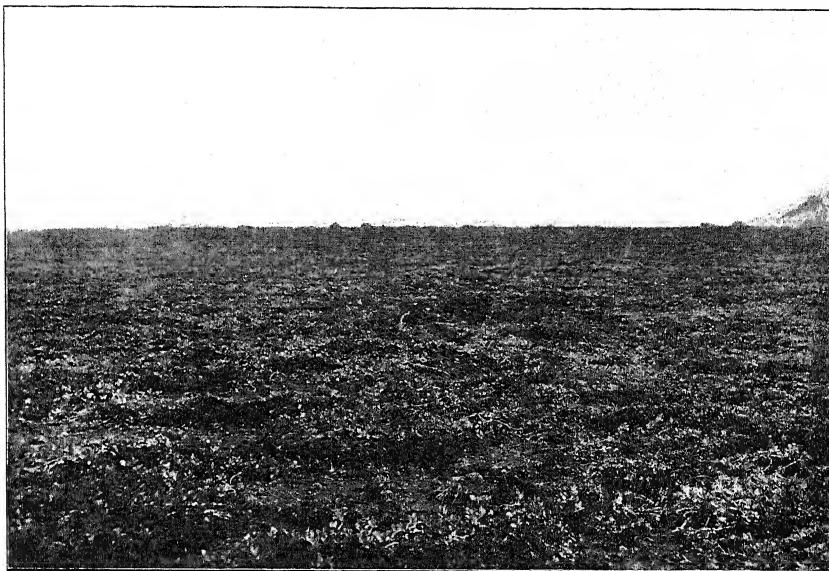


Fig. 18. The *Betula nana*-Mo on Arnarvatnsheiði.

Surface covered with vegetation but without knolls. For the composition of the vegetation
see table 22 A, 7—11, pp. 104—105.



Fig. 19. The knolly Mo on Arnarvatnsheiði.

Surface knolly. For the composition of the vegetation see table 23 A, 1—5, pp. 107—108.



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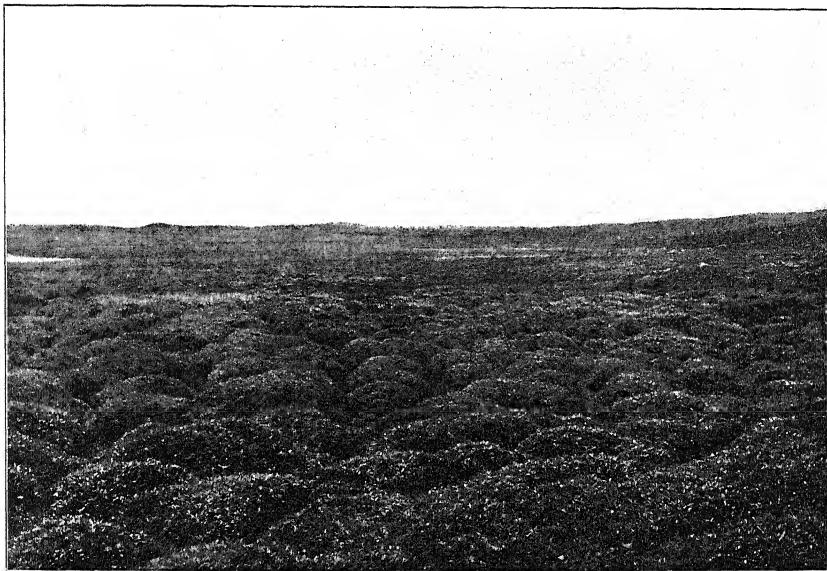


Fig. 20. The Jaðar Vegetation on Arnarvatnsheiði.

Surface covered with large knolls and a vegetation the composition of which is shown in table 23 A, 6—10, pp. 107—108.



Fig. 21. Picture of a Depression with Mýri on Arnarvatnsheiði.

The varied composition of the highland mýri is illustrated by the collections of water.
For vegetation see table 24 A, p. 112.

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Fig. 22. A portion of the Flói on Arnarvatnsheiði shown in fig. 21.
Surface without knolls. For vegetation see table 23 A, p. 112.

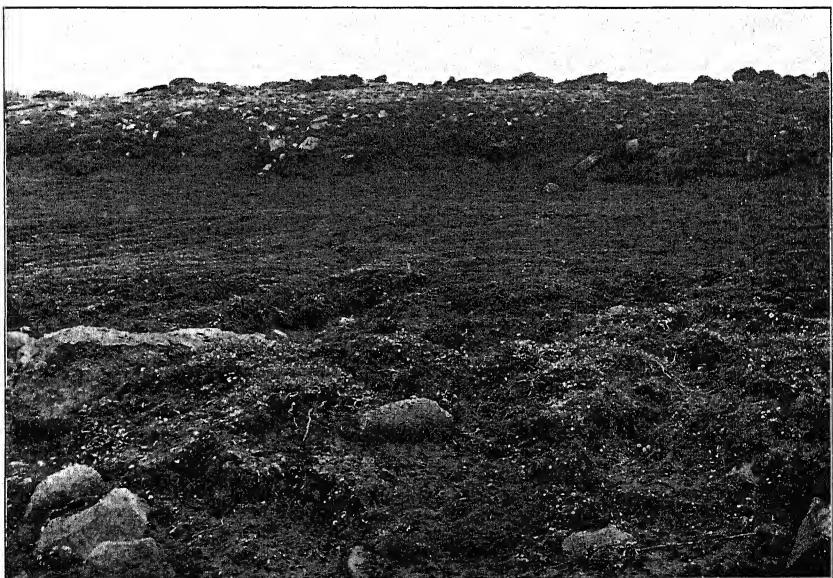


Fig. 23. Strip of Snow Patch, on the north aspect of a hill.
In contrast to the formations above and below, the surface is comparatively level.
For vegetation see table 25 A, 5, pp. 116—117.

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Fig. 24. Large Patch of Snow on Arnarvatnsheiði.

Surface level, the vegetation differs on the bottom and sides of the snow patch.

See table 25 A, pp. 116—117.



Fig. 25. A portion of the Patch shown in fig. 24.

Geranium sylvaticum in bloom.

plants but prompt in others, and it is possible that drouth resistance is largely a matter of the relative ability of the plant to keep its stomata closed under the stimulus of high temperatures.⁴⁵³

The roots of plants in undisturbed soil are generally deep enough to escape injury due to excessive heat, but where plants are grown in containers, the direct insolation of the containers becomes an important factor because roots tend to be concentrated in a layer against the inside walls. Shielding such containers from sunlight, or immersing them in a water bath, will guard against this undesired effect.

Temperature and Plant Diseases¹¹³

The ability of a parasitic fungus to gain entrance into as well as to develop within a host organism is often strongly conditioned by temperature. For example, at temperatures below 13° C the seedlings of most strains of maize become very susceptible to disease, whereas flax becomes susceptible to *Fusarium* wilt only at temperatures above 14° C. Host plants commonly extend into climates where temperature restricts their parasites,⁷¹¹ and it is often possible to subject a diseased plant to temperatures lethal only to its parasite.

The Time Factor in Temperature Relations

The rate of temperature change is often fully as important as the degree of change. Sudden changes tend to be more deleterious to plants than slow changes of the same magnitude, apparently because the protoplasm requires a certain amount of time to adjust itself to new temperature levels. It will be recalled that the rate of cooling, rather than the absolute minimum, determines whether or not the plant is injured by the formation of intracellular ice or the development of stem lesions. Likewise, the temperature extremes that result in sunscald are no greater than the extremes endured at other times when the change from high to low temperature is more gradual. Tissues of an insolated leaf may be killed in spots where drops of cool water fall on them.¹⁸⁶ Injury associated with freezing is sometimes increased when temperatures drop rapidly, or when the tissues are thawed rapidly.⁴⁴⁵ Under natural conditions such injury may result from the fact that the conditions bringing about rapid thawing at the same time cause a sudden increase in transpiration stress. Although the relative importance of tempera-

ture and concomitant variables is difficult to assess, it may be true that certain plants confined to protected habitats are excluded from others because of more rapid temperature fluctuations there.

Within certain limits rapid rates of temperature change may be of benefit to plants. Certain species will not flower unless the plant experiences a rapid drop in temperature, the same differential being without effect if accomplished over a longer period.

It has been demonstrated that, when a plant is transferred from one environment to another with a different temperature, the rate of physiologic processes quickly changes, but the new level of activity is not long maintained. Also, when a lot of seeds is divided and placed under conditions suitable for germination but at different temperature levels, a well-marked optimum is evident at first, but as time advances satisfactory germination is secured over a much broader range.¹⁸² Consequently germination percentages and cardinal temperatures must always be defined in terms of duration as well as level (Fig. 45).

Time also has an important bearing upon the degree of injury sustained at extreme temperatures. A plant may withstand an extreme of a given intensity for a short time, whereas the same temperature maintained for a longer period would prove fatal (Fig. 50). The giant cactus (*Cereus giganteus*) can tolerate no more than 18 hours of temperature below freezing, and this restricts its natural distribution.⁶¹³ This phenomenon may be explained in part by the

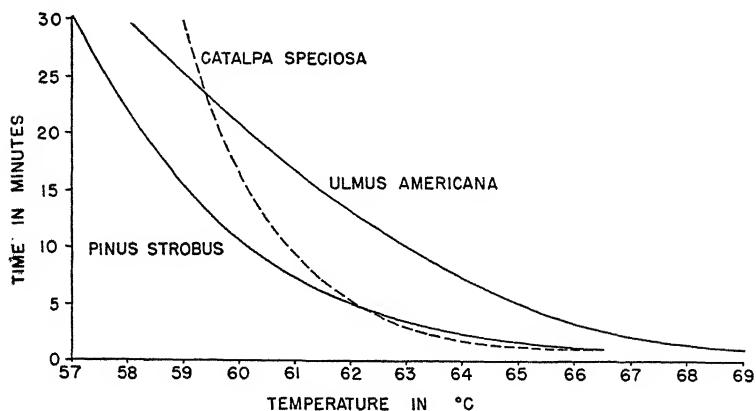


Fig. 50. Time required to kill cortical parenchyma cells at different temperature levels. (After Lorenz, 1939.)

fact that, owing to undercooling, plant tissues may not freeze until critical temperatures have prevailed for some time. The length of time in the frozen state, within certain limits, seems to be of no great importance. In this connection the time factor can be expressed as the number of consecutive hours at or below a certain level, or as *hour-degrees* of freezing weather in which intensity as well as duration is taken into consideration. Sometimes brief interruption of a cold period may nullify its effects.⁶³⁶

Temperature and Plant Geography

In the preceding discussions evidence has been presented that temperature limits the ranges of plant species directly or indirectly as follows:

1. Poleward or upper altitudinal limits are set by:
 - a. Extremes so low as to kill the protoplasm.
 - b. The relative efficiency of summer heat in respect to the accumulation of carbon compounds.
 - c. The relative adequacy of summer temperature to stimulate reproduction.
 - d. Parasites that become active only at low temperatures.
 - e. Adverse combinations of day and night temperatures.
2. Equatorial or lower altitudinal limits are set by:
 - a. Extremes so high as to kill the protoplasm.
 - b. The photosynthetic-respiration relationship.
 - c. The inadequacy of winter temperatures to stimulate germination, growth, and sexual reproduction.
 - d. Parasites that become active only at high temperatures.
 - e. Adverse combinations of day and night temperatures.

In addition to these major aspects of temperature, numerous special but indirect relationships may be significant. For example, the hypothesis has been suggested that forest extends into arctic tundra only along river valleys because of the snow accumulations there which protect the soil from freezing deeply at an early date in winter.

Actually many other factors, climatic, edaphic, or biotic, frequently prevent a plant from attaining its theoretical maximum range with respect to temperature requirements. Significant in this respect is the fact that the geographic area over which individual crops may be grown usually takes the form of a belt elongated in an east-west direction, but such a distribution pattern is much less pronounced in regard to the natural ranges of plant species. This indicates that

cultural practices can accomplish much in the way of making other conditions suitable for plant growth, but temperature limitations are less easily overcome.

It has long been known that when equal areas are considered, the number of plant species increases in an equatorial direction from both poles. Although other factors such as relative stability of climate and land masses have undoubtedly played an important part in bringing about this condition, the north-south temperature gradient may have had something to do with the rate of evolution. Under experimental conditions, at least, the rate of mutation has been found to increase directly with temperature.

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Our understanding of any environmental factor is fundamentally conditioned by the degree of refinement in the methods employed in measuring that factor. Not only must the number and distribution of measurements be adequate from a statistical standpoint, but also in the interpretation of data it is essential that the limitations of each instrument be understood. It is easy to accumulate great quantities of data, but it is not easy to determine with precision the temperature of most objects, surfaces, and media. There follows a brief discussion of the principal instruments used in measuring temperature in ecologic studies, together with suggestions concerning their application.

Simple Thermometers

Ordinary mercury-in-glass thermometers can be used for instantaneous determinations of temperature in places where there are no sharp temperature gradients. They can be inserted in water, in soil, and into thick plant organs. If they must be removed to be read, this must be done with alacrity, for the mercury column begins to change noticeably within a second or two.

These thermometers should never be used for soil temperatures except at some depth on account of the sharp temperature gradients near the surface (Figs. 38, 40). A pointed steel rod with a diameter slightly larger than the thermometer is useful in making a hole in the soil to the depth to which temperature is to be measured. If used in tubes inserted in the soil,^{182, 218} the bulbs can be insulated

with a coating of paraffin to reduce their rates of temperature change when removed for reading.

Thermometers are generally calibrated quite carefully by the maker, but the frequency with which these instruments develop unexplainable inaccuracies serves as a caution against using any one of them indefinitely without checking its precision.

True air temperatures can be approximated most closely only if the sensitive element of the apparatus used is protected from direct sunlight and sky light in a well-ventilated shelter large enough so that the element is at least 3 dm from any side of the box.⁵⁵² However, the points must not be overlooked that in ecologic work the tissue temperatures are the critical values, and plant organs are subject to strong radiational loss of heat at night as well as direct and indirect insolation during the day. Temperatures as obtained in an instrument shelter are buffered against radiation and isolation so that they never rise as high or drop as low as plant temperatures. For this reason some have proposed using more direct exposure of instruments with a view to getting a closer approximation of tissue temperatures.⁷⁵⁰

Maximum-Minimum Thermometers

A common and widely used apparatus that makes automatic records of maximal and minimal temperatures consists of a pair of thermometers, one mercurial and one alcoholic. The bulb of the former is mounted a few millimeters higher than the stem; the latter is tilted the same amount in the opposite direction. The bore of the mercurial member is constricted just above the bulb to such an extent that, although rising temperature can still force mercury from the bulb into the bore, the extruded mercury cannot return. Thus this thermometer registers the maximal temperature until it is reset by centrifugal whirling, which forces the excess mercury in the bore back into the bulb. Since the mercury column is broken at the constriction, the thermometer must be gently turned to an upright position to read the correct value.

In the alcoholic member there is a short, thin rod of metal in the extremity of the liquid column. This rod, or index, is light enough so that a receding meniscus will draw it back toward the bulb as temperature drops, but there is no force to cause it to move back if the alcohol should subsequently expand. The position of the distal end of the index then indicates the minimum temperature, and

the instrument is reset by tilting so that the metal index slides down the bore and rests against the meniscus once more.

Another (Six's) type of maximum-minimum thermometer has a U-tube with a central section of mercury, colorless creosote filling the remainder of the bore except for a bubble of air at one end to accommodate expansion and contraction. The mercury column moves forward and backward with each change of temperature, pushing an index at either end. Friction prevents the indices from moving back as the mercury recedes so that one index records the maximal and the other the minimal temperatures. A magnet is used to pull the indices back against the mercury column and reset the instrument. Costing approximately half as much as the pair of thermometers described above, and being slightly less fragile, Six's thermometer is generally the more satisfactory for field work.

Although usually employed in connection with air temperatures, maximum-minimum apparatus has also been used to study water and soil temperatures.^{218, 678}

The "mean temperatures" reported by the U. S. Weather Bureau are in reality medians based upon daily readings of a pair of maximum-minimum thermometers. As approximations of true mean temperatures these leave much to be desired, for the median is usually higher than the mean, and the "mean" based on maximum-minimum record may be as much as 2° F in error.¹⁸³

Thermographs

A continuous record of temperature is frequently an essential part of experimentation, for, as previously discussed, the duration of different temperature levels is often of much significance. *Thermograms* obtained by instruments called *thermographs* provide the only adequate data for calculating temperature efficiency, and they are the perfect records of the degree of constancy secured in "constant"-temperature apparatus. This instrument is also invaluable in obtaining temperature records at stations that cannot be visited more often than once a week.

The most popular form of air thermograph at present has a sensitive unit consisting of a flattened, curved, metal tube filled with liquid. Changes in temperature alter the curvature of this tube. One end of it is fixed, and the other motivates, by lever mechanism, a pen that moves across a paper chart furnished by the instrument maker. The chart, marked off in degrees, hours, and days, is wrapped

around a drum. The drum is motivated by a clock movement and makes one revolution in seven days. These instruments are advertised as being accurate to 0.5° F, but it is essential that a maximum-minimum thermometer be kept in the instrument shelter so that the degree of inaccuracy can be recorded and suitable corrections applied to the data taken from the thermogram. Instruments are on the market that make two records at once on the same chart, such as air temperature and soil temperature or air temperature and relative humidity. At each visit the chart must be changed, any correction data recorded on the thermogram, and the actual date written on the new chart as it is installed. The clock must be wound and then the drum rotated by hand until the pen is on the correct line. If necessary the pen should be refilled with ink (a glycerine solution of dye is satisfactory); then capillary connection must be established between the ink drop and the paper through the leaves of the pen. Whenever it is necessary to readjust the pen to indicate a more correct temperature, the instrument should first be allowed to attain a perfect equilibrium with the air.

The sensitive unit of the soil thermograph is a cylindrical tube about 27 mm in diameter and several decimeters in length. Because of its size it should be used only below about the 2-dm level. The large bulb, filled with toluol, is connected by means of a flexible cable to the recording mechanism, and, since both the cable and the recording mechanism are sensitive to temperature changes, accuracy is insured only when the cable is buried at approximately the same depth as the bulb, and the drum housing is placed in a covered box sunk in the earth.^{441, 688} The pen is adjusted after observation of the soil temperature at the level of the bulb some time after the bulb has been in place.

Thermocouples ^{183, 577}

Because the sensitive elements of most of the instruments described above are at least several millimeters in diameter, none is suited to measuring the temperature of small areas where the gradient is steep. The only instrument adequate for measuring the temperature of the cambium layer, the inside of a leaf, the very surface layer of soil grains, etc., is the *thermocouple*. This is made by fusing together in a Bunsen flame the ends of two fine wires of dissimilar metals, usually copper and constantan (an alloy of copper and

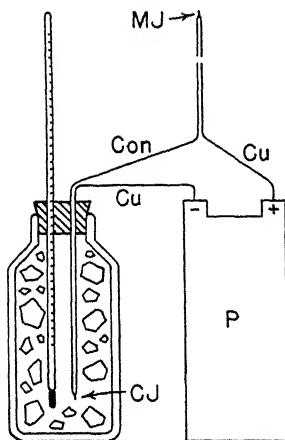


Fig. 51. Diagram of a thermocouple made of copper (*Cu*) and constantan (*Con*) wires connected to a potentiometer (*P*). The cold junction (*CJ*) is in a thermos bottle of chipped ice. Below the measuring junction (*MJ*) there have been omitted long segments of the wires which make the apparatus more convenient to use.

nickel). At the junction of these metals a difference of electrical potential is set up, and the magnitude of this difference is proportional to the temperature of the junction. Two such junctions are connected in series, one being kept at a known constant temperature (such as 0° C in a thermos bottle of distilled water containing crushed ice), and the other being placed where the temperature is to be measured (Fig. 51). The thermocouple is also peculiarly adapted to measuring the temperature of water at considerable depth, and a more substantial type of junction can be made which can be thrust into the soil at various depths.⁴⁴¹

A potentiometer is used to measure the differences in potential between the two junctions, and temperatures can be read off prepared tables.

Thermistors^{433, 531, 539}

Thermally sensitive resistors (*thermistors*) are instruments somewhat similar to thermocouples in that a potentiometer is used to measure the resistance offered to an electric current passing through an extremely small globule composed of a sintered mixture of metallic oxides. Advantages claimed for this instrument over the thermocouple are: (a) length of wires between measuring junction and potentiometer has no effect on readings, (b) a reference junction at known temperature is not needed, (c) greater sensitivity, and (d) lower cost of apparatus. On the other hand, for field use the

sintered globule must be in a moisture-free housing so that the sensitive element is much larger than the fine point of a thermocouple.

Sucrose Inversion

If a sterile, freshly prepared solution of sucrose is sealed with some enzyme in a small glass capsule, inversion to monosaccharides is subsequently proportionate to temperature efficiency. A polarimeter is used to compare the relative amounts of monosaccharides at the beginning and end of a time period. This method of temperature evaluation has the advantage of automatically integrating the different efficiencies of different levels on the temperature scale, but has the disadvantage that the Q_{10} of inversion is not variable as is the Q_{10} of plant processes. Furthermore, the method is comparative, and the results cannot be equated with the usual type of temperature data.

Melting-Point Indicators⁶²³

Wax shavings, or bits of other solids with narrow ranges of melting point, may be laid on insulated surfaces to indicate by changes in their shape whether or not temperatures rise to specific levels.

Biologic Methods

Despite the fact that the seasonal progress of plant development is influenced by a number of factors, phenology constitutes a method of evaluating the earliness or lateness of seasonal temperatures which has certain advantages over direct measurements of weather variables. From phenologic data maps can be drawn with lines (*isophenes*) connecting locations where plants are in the same stage of development at the same time. This biologic method has been found very useful in Europe but has not yet been applied to any extent elsewhere. In using the method species must be selected that are insensitive to daylength (see discussion in Chapter Five).

Temperature Control

Temperature control for seeds and heterotrophic organisms which do not need light is not particularly complicated provided that refrigerating and heating units with suitable thermostats are available.

The same applies to studies where only soil temperature need be controlled.³³⁰

Studies of the influence of air temperature on the shoots of green plants, however, demand units of larger size. Some source of light must be provided during part of each day, and the relative humidity must be controlled.^{67, 80, 229, 675, 735} Relative humidity is regulated in accordance with the various temperature levels in such a manner that the saturation deficit is uniform throughout.

When it is desirable to alternate temperatures from a low level at night to a higher one during the day, a satisfactory practice is to move the plants back and forth between two chambers set at the desired temperatures. The high-temperature period in this case should never exceed 8 hours.²⁶¹



CHAPTER FIVE

The light factor

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The energy necessary to sustain life on earth is derived from sunlight directly by green plants, or indirectly by other organisms which, except for chemosynthetic bacteria, must eventually depend upon organic compounds synthesized by green plants. Chlorophyll, through its ability to absorb radiant energy from the sun and convert it into chemical energy contained in simple sugar molecules, provides the essential connecting link between nearly all living organisms and solar energy. In addition, light exerts many stimulating effects upon plants, especially upon the differentiation of tissues and organs. In fact, light is rivaled only by water in its influence upon the morphology and anatomy of plants. Less evident, but certainly none the less important, are the effects of light on the physiologic processes and chemical composition of plants.

SUBDIVISIONS OF RADIANT ENERGY AND UNITS OF MEASUREMENT

All radiant energy the earth receives from the sun is in the form of electromagnetic waves varying in length from about 5,000 to 290 millimicrons.* This series, the *solar spectrum*, can be conveniently subdivided on the basis of wavelength as follows.

Light

Wavelengths between approximately 750 and 400 millimicrons are called *light* or *luminous energy* because these alone out of the total range of wavelengths can be seen with the eye (Fig. 52). This is likewise almost the entire range of wavelength involved in photo-

* One millimicron ($m\mu$) = 0.000001 mm = 10 Ångström units (Å).

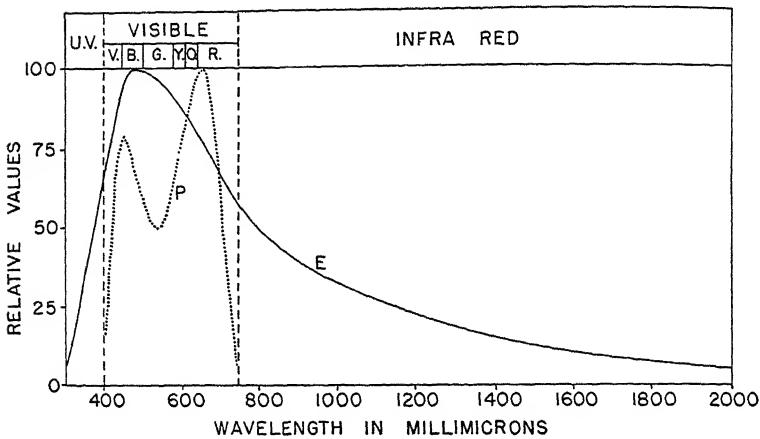


Fig. 52. Distribution of energy (*E*) in the solar spectrum at the earth's surface, and the relative rates of photosynthesis (*P*) of wheat in different wavelengths of light of equal intensities. The inefficiency of green light is simply a consequence of reflection and transmission reducing utilization.⁷²³ (*E* after Fowle, 1927; *P* after Hoover, 1937.)

synthesis, and green plants grow normally only when exposed to a combination of most of the wavelengths in this range.^{522, 600} Approximately 50% of the total energy of solar radiation lies within this narrow range.

When sunlight is passed through a prism it is dispersed into a series of wavelengths exhibiting different colors as follows: red 750–626 millimicrons, orange 626–595, yellow 595–574, green 574–490, blue 490–435, violet 435–400. All these colors making up the *visible spectrum* affect photosynthesis, but yellow and green are utilized very little, the principal wavelengths absorbed lying in the violet-blue and orange-red regions (Fig. 52). Phototropism is governed chiefly by blue-violet wavelengths.

Infrared Radiation

In this category are included wavelengths longer than the longest to which the eye is sensitive—hence the name infrared, meaning “below red.” Animals can detect the presence of this type of energy only by the sensation of heat which it produces, the longer the wavelength the greater being its heating effect. Infrared radiation is

not powerful enough to stimulate chemical reactions, and so is of most ecologic importance from the standpoint of its heating effects; however it appears to exert a stimulating effect on stem growth and germination that is unrelated to its heating property.⁷²³

Ultraviolet (Actinic) Radiation

Wavelengths less than 390 millimicrons are too short to be seen (ultraviolet meaning "above violet"), but they are very active in certain chemical reactions. Plants do not require these wavelengths for normal growth and in general are not injuriously affected by them.⁵³⁶ Owing to the screening effect of ozone in the atmosphere they comprise but about 2% of radiation at the earth's surface. Furthermore the epidermis is essentially opaque to these rays. For these reasons ultraviolet radiation is not particularly important except to certain of the lower plants. Wavelengths shorter than those found in sunlight are definitely injurious.

Ultraviolet, and to a certain extent the shorter wavelengths of light as well, tend to promote the formation of anthocyanins, are responsible in part for phototropic phenomena, and by inactivating growth-promoting hormones check stem elongation.

For the sake of convenience, and because of its relatively minor importance, the effect of ultraviolet on plants will be considered along with light in this chapter.

Units of Measurement

The gram-calories unit of energy measurement, when applied to radiant energy, sums the effects of invisible radiation as well as of light. When dealing with very small quantities of energy the *joule* or *erg* is used. One gram calorie = 4.18 joules = 41.8 million ergs.

Measurement of the intensity of light alone is based on the illumination produced by a *standard candle*. Actually candles are no longer used, having been replaced by less variable standards, but the term *candlepower* has been retained for the units. The amount of light received at a distance of 1 m from a standard candle is called a *lux* (*L*) or *meter candle* (*M.C.*). The light intensity at 1 foot from a standard candle is called a *foot-candle* (*F.C.*), which equals 10.764 *L*. By common agreement of world scientists the lux has been

accepted as the standard international unit for expressing light intensity. Light energy can be expressed as lux-seconds or lux-hours, for according to Bunsen and Roscoe's law a definite photochemical effect requires a definite amount of light energy regardless of its distribution in time.

Aside from the above type of absolute expression of light intensity, it is often convenient to express the amount of light received under water or vegetation as a percentage of the amount received where these screening influences are not operative.

The basis of comparison here (full sunlight) is not a fixed intensity but varies greatly with the season, the time of day, humidity, and other atmospheric factors.⁵⁵ However, this limitation is more important to the physiologist than to the ecologist, for plant response to specific light intensities under laboratory conditions is not adequate to explain shade tolerance in the field. Percentage values made in the field automatically nullify the influence of a swarm of variables other than light energy which influence plants growing in the shade, and which are too complex to duplicate under laboratory conditions. It is the *balance* between production and use of metabolites, as influenced by *all* shading influences, that is critical for field survival.

RELATIVE IMPORTANCE OF QUALITY OF LIGHT

As with the temperature factor, light varies in intensity and duration, but unlike temperature it also varies in quality, i.e., the proportions of red, yellow, blue, etc. For practical reasons, however, this complication remains chiefly of theoretical importance in plant ecology. It is not feasible to place much importance upon variations in wavelength under natural conditions for the following reasons. (a) Although it is true that variations in quality affect plant processes differently, each process is somewhat sensitive to all wavelengths of light, so that in ecologic work analyses of wavelength composition are difficult to interpret. (b) The influence of light quality upon plants differs so much from one species to another that, with the exception of those generalizations already mentioned, no other physiologic roles of different portions of the spectrum have yet been established. (c) With land plants growing under natural conditions the variations in light quality have never been demonstrated

to be great enough to be critical as an environmental factor. For these three reasons the intensity and duration of light are the variables of chief ecologic importance.

SPATIAL VARIATIONS IN LIGHT INTENSITY

Effects of Atmosphere

Atmospheric gases, chiefly nitrogen and oxygen, absorb and disperse a small portion of the shorter wavelengths of light as it passes through the gaseous layer enveloping the earth.* ✓ The higher the elevation of a surface above sea level, the thinner the layer of air remaining above it, and the brighter the light. Mountain summits extending to an elevation of 2 miles are exposed to a maximum intensity of about 129,000 L whereas only 107,000 L are received at sea level. However, unless strongly influenced by cloud and fog, differences in light intensity due to elevation are not of sufficient magnitude to be of critical importance to plant life.

In contrast to N and O, all moisture contained in the air, visible as well as invisible vapors, exerts a powerful screening effect. For this reason the intensity of light is much greater in dry than in humid climates and is very low where cloud and fog are abundant as along the central and northern Pacific coast of North America or in tropical mountains. On a cloudy day light may be reduced to 4% of the normal intensity. Under these conditions a relatively high proportion of the longer light rays and infrared rays are absorbed by the moisture, and the shorter light rays and ultraviolet are scattered. Light scattered by gas molecules and water droplets becomes *diffuse light* or *sky light* as contrasted with *direct light*. On clear days diffuse light comprises but 10–15% of the total light, whereas on overcast days it may comprise up to 100% of the total.⁶⁰²

As pointed out in connection with heat, the angle of the sun's rays with respect to the earth's surface at a given point determines the distance which the rays must pass through the atmospheric blanket to reach that spot and likewise determines the amount of surface over which a given amount of light is spread. Latitudinal variations in light intensity due to the height of the sun above the horizon are

* It is due to this absorption that ultraviolet wavelengths shorter than 290 millimicrons never reach the earth's surface.

very important. In equatorial regions light is most intense and contains the highest proportion of direct sunlight. Progressing toward the poles the intensity decreases and the percentage of diffuse light increases.

Effects of Layers of Water

Submerged plants are subjected to weaker illumination than terrestrial ones, for part of the light is reflected back at the water surface, and of the remainder much is absorbed by the upper layers. The greenish or bluish color of bodies of water indicates that the principal wavelengths reflected are at the short end of the spectrum, especially between 420 and 550 millimicrons. When the surface of water is rough reflection is increased several times.

As light penetrates water the intensity decreases geometrically as depth increases arithmetically. Even in perfectly clear water only 50% of the light impinging upon the surface penetrates as far as 18 m, and at 50 m there may be barely sufficient light (approximately 0.0000001%) for feeble photosynthesis. More than half the earth's surface lies in perpetual darkness, beyond the reach of sunlight, under half a mile or more of ocean water.

Light penetration through snow often is sufficient to allow hardy plants to begin growth before the snow cover melts in spring. Photosynthesis may take place under as much as 40 cm of snow, although the condition of the snow may be such that much less light gets through.²¹⁹

Effects of Suspended Particles

Solid particles dispersed in the air (dust, smoke) or in water (clay, silt, plankton, bog colloids) have a great screening effect.

Turbidity in streams draining arid regions is often inevitable because of the sodium ions which cause colloidal dispersion. Streams from limestone regions tend to remain clear most of the time because of the flocculating action of calcium ions. Owing to accelerated erosion brought about by man, many streams which would otherwise be clear are so heavily laden with colloidal soil particles that submerged plants, and consequently the animal life dependent upon them, have disappeared.

In metropolitan areas smoke may cut off 90% of the light. Even more detrimental are the effects of smoke particles which settle out

of the air and accumulate as films on plant surfaces. This not only cuts down the amount of light available to the chlorenchyma but partly plugs the stomata as well. Plants with sticky or hairy surfaces suffer the most. Also evergreens are inherently more vulnerable to this form of injury than deciduous plants which use their leaves for only a few months, although exceptional evergreen plants are tolerant and deciduous plants sensitive to smoke films. In England evergreen conifers cannot grow where more than 50 tons of soot are deposited per square mile per year, and deposition in industrial areas may amount to 539 tons.⁵⁸⁸ Even clean glass oriented at right angles to the light rays cuts out about 13% of sunlight, and when allowed to collect grime the interception may rise to several times this value.

Effects of Layers of Vegetation

Leaves transmit about 10% of the light impinging on them, so that most of the light that penetrates through foliage passes between the leaves as sunflecks or as sky light.⁵⁸⁹

In evergreen coniferous forests the quality of light is scarcely affected by this screening action of the foliage, but in winter-deciduous forests the quality of light that has filtered through the leafy canopy differs materially from full sunlight: the proportion of red light is higher, and the proportion of blue and violet is lower.²² As far as is known these differences have no influence in determining the differences in undergrowth between these two kinds of forests, apparently the increase in proportion of long wavelengths offsetting the decrease in short wavelengths.

In a complex plant community, the stature of any one plant in relation to that of its neighbors determines to a large extent the amount of light it receives. In a forest only the mature trees of the tallest species ever receive full insolation. Undershrubs receive subdued illumination; herbs and especially epigeous cryptogams grow in still weaker light.⁶⁰⁵ When in full leaf the canopy of very dense forests may reduce light to less than 1% of full sunlight. No autotrophic plants can live under such conditions, and the ground frequently remains bare until the death or injury of one or more of the trees improves lighting.

The reduction of light by a canopy of vegetation is very important ecologically, particularly after the intensity is reduced to about 20%, but, because other factors such as wind, relative humidity, soil

moisture, and temperature vary concomitantly with reduction in light intensity (Table 6), it is extremely difficult to evaluate the influence of the light factor alone.⁶⁰⁸ It must therefore always be remembered that the word shade connotes a complex of factors.

Effects of Topography

The direction and slope of the land surface caused marked variations in the intensity and daily duration of insolation. In general the temperature aspect of this topographic factor is probably more important than the light aspect. However, on steep poleward slopes direct sunlight may be completely lacking at noon so that plants must rely heavily on sky light, which is only about 17% as intense as the light received by a surface level enough to get full direct lighting. To get the maximum possible sunlight a plant must grow where neither topographic nor other features of its surroundings are near enough or high enough to interfere with sky light from any direction.

TEMPORAL VARIATIONS IN LIGHT

At dawn, at sunset, and in winter, light intensity is weak because the waves are traveling a long distance through the atmosphere and most of the light, especially the shorter wavelengths, is absorbed. When the sun is at the horizon the rays pass through approximately 20 times the thickness of the air they have to penetrate when the sun is overhead. For this reason the diurnal intensity is represented by a broad curve reaching a midday maximum at which time direct sunlight furnishes up to about 83% of the available energy, and tapering rapidly to weak light at either end where sky light becomes the sole constituent (Fig. 16). It is to be noted that effective daylength is not limited to the period between sunrise and sunset, for the sky light available before sunrise and after sunset is of considerable ecologic importance.

Winter sunlight in central North America is only one-tenth as bright as that of summer.

At the equator daylight prevails for about 12 hours out of every 24, in both summer and winter. Progressing toward the poles the length of day (i.e., the *photoperiod*) becomes increasingly longer than 12 hours in summer and increasingly shorter than 12 hours in winter. Even within the range of latitude encompassed by the

United States daylength at the summer and winter solstices differs about 2 hours between the southern and northern tiers of states. Above the latitude of about 66° effective daylight in midsummer lasts through the 24-hour day, whereas in midwinter only faint indirect light is seen for a short period centering about noon.

Illumination in microclimates fluctuates hourly. Under a canopy of vegetation the movement of leaves by the wind, together with the variations in the movements of sunflecks and shadows across the ground, results in rapid and wide variations in the amount of light energy received at a given point. Thus, the light intensity at a leaf surface may rise abruptly from 2% to 35% for a few minutes and then drop to its former low. Because of the influences of wind, changing angle of the sun, differences in time of day and of season, and the effects of weather, single measurements of light intensity under a vegetation canopy cannot be interpreted very closely.⁸⁸

The turbidity of water, and hence its transmission of light, varies greatly with the amount of wind action.¹⁰³ Likewise the effect of plankton on light penetration through water is very different depending upon seasonal variations in light, temperature, and aeration. Wide fluctuations in water transparency result from these superimposed influences.

Moonlight is bright enough (to 0.2 L) to satisfy light requirements of certain seeds,³¹⁵ to promote starch hydrolysis in leaves, to affect leaf movements of legumes, and possibly to stimulate sexual activity in certain marine algae.^{37, 595}

IMPORTANCE OF LIGHT TO PLANTS

Light affects a number of plant functions, and, like temperature, the positions of the cardinal values tend to vary with the particular function, the kind of plant, the stage of the life cycle, and with variations in other factors.

Photosynthesis

The basic pattern of the plant shoot is directed toward efficiency in photosynthesis. The stem functions as a support enabling leaves to be exposed advantageously to light, and the large surface of the thin photosynthetic organs favors the absorption of light energy. The structure of the spongy mesophyll and the stomatal apparatus

allows rapid gas exchange. Even the fact that photosynthesis utilizes the visible wavelengths of radiation most heavily is significant, for this is the region of the spectrum with the greatest energy values. Despite this apparent efficiency, full use is never taken of all the light energy, and under full insolation there is a tremendous excess of unused light. On the average actively growing land plants use only about 1% of visible radiation in photosynthesis.⁵⁴⁴

Respiration is a never-ending process in every protoplast, by which carbon compounds are oxidized to liberate energy for the maintenance of vital activity. Whenever a plant is not carrying on photosynthesis its dry weight progressively decreases as a result of respiration. The amount of light required for photosynthesis to equal the respiratory use of carbon compounds, i.e., for CO₂ to be neither absorbed nor evolved, is called the *compensation point*. This value is always higher than the absolute minimum for photosynthesis, varying from about 27 to 4,200 L⁶²⁸ in higher plants. With tree seedlings the value usually lies between 2 and 30% of full sunlight (Table 11).

Table 11

Compensation points of some tree seedlings based on 3-hour tests of potted plants. Values are percentages of full winter insolation in Maine as measured with a thermocouple.⁵⁹

<i>Pinus ponderosa</i>	30.6	<i>Celtis occidentalis</i>	11.5
<i>P. sylvestris</i>	28.7	<i>Picea engelmannii</i>	10.6
<i>Thuja occidentalis</i>	18.6	<i>Pinus strobus</i>	10.4
<i>Larix laricina</i>	17.6	<i>Picea abies</i>	8.7
<i>Pseudotsuga menziesii</i>	13.6	<i>Tsuga canadensis</i>	8.4
<i>Pinus contorta</i> var. <i>latifolia</i>	13.6	<i>Fagus grandifolia</i>	7.5
<i>Quercus borealis</i>	13.6	<i>Acer saccharum</i>	3.4

During protracted cloudy weather photosynthesis may lag behind respiration needs and food reserves decline to the extent that animals depending on forage starve.¹⁸⁵

Growth obviously demands synthesis in excess of respiration, so that the minimum requirements for this function are met only when light intensity exceeds or has exceeded the compensation point. Thus the compensation point for seedlings of *Pinus strobus* is 1,830 L, but twice this amount of energy is required to maintain growth.²³⁷ An increase in light causes a small increase in the respiratory rate as well as the photosynthetic rate, and therefore raises the light value of the compensation point. Still, the net effect of light increase at low intensities is highly beneficial, for the rate of photosynthesis increases so much more rapidly than the rate of respiration.

For most plants the optimum light intensity for photosynthesis appears to be considerably less than full sunlight as far as the individual leaf is concerned. However, when a large plant grows in full sunlight a great many leaves do not get enough light for maximum photosynthesis owing to shading by other leaves and to leaf orientation in relation to the directions of incident light.¹¹² Because of this, full sunlight may benefit the leaves within the canopy enough to more than offset the effect of supraoptimal lighting of the fully exposed leaves, and as a result the plant as a whole may assimilate most rapidly when growing in full sunlight. The rate of photosynthesis in apple trees, for example, increases to the maximum at full insolation, although in a single leaf blade this function progresses most rapidly between 25% and 33% of full sunlight.²⁸⁰

Unicellular green plants can survive in habitats where light is too weak for multicellular plants, simply for the reason that in the latter group each chlorenchyma cell must not only manufacture the food it requires for itself but must provide an excess for the nonphotosynthetic cells. The compensation points of simple algae are therefore lower than for differentiated plants,⁶⁰⁷ and they utilize a higher percentage of light energy (as much as 10%).

The expression optimum light intensity used for plants growing in natural habitats does not imply that the intensity is really optimum for photosynthesis except at fleeting intervals. Much of the time and for most of the photosynthetic organs sunlight is either too weak or too intense for maximum assimilation. Optimum means only that under certain combinations of habitat factors the net effect of lighting conditions over a considerable period of time is more favorable for photosynthesis than it is under other combinations.

Heliophytes and Sciophytes

Plants may be classified ecologically according to their relative requirements of sunlight or shade. Those that grow best in full sunlight are called *heliophytes*, and those that grow best at lower light intensities are *sciophytes*. Among heliophytes there are some species which, though they grow best in the sun, can grow fairly well under shade. These are called *facultative sciophytes*, and those sun plants which cannot do so are *obligative heliophytes*. Sciophytes likewise can be divided into two groups, depending on their relative ability or inability to tolerate full sunlight.

With most submersed aquatics no difficulty is involved in assessing

the importance of the light factor,^{585, 682} but in terrestrial habitats other factors, especially temperature and relative humidity, vary concomitantly with light intensity and it is very difficult to evaluate light effects alone. In fact, investigators have frequently concluded that the failure of seedlings under light intensities that appear to be critically low is really due to shade factors other than light. Also, in assessing the value of the light factor it must not be overlooked that photosynthesis is not the only function requiring light. In consequence an explanation of the relative difference in success of heliophytes and sciophytes in sun and shade is complex, resting on the net influence of a galaxy of concomitant variables operating on a series of interdependent plant functions.

In certain species, as in the apple trees discussed above, light requirements for photosynthesis may alone offer sufficient explanation of their superior growth in full sun. Inadequate light energy has a directly detrimental influence when respiratory requirements are not sufficiently exceeded, but the effects may also be indirect. For example, when insufficient light is available and photosynthesis is curtailed the roots of plants suffer the most restriction of growth, and the inadequate root systems in turn jeopardize the continued welfare of the plants. Also, in some instances soil drouth in the surface horizons is more severe in full sun than under shade, but the more rapid penetration of seedling taproots in the sun may more than offset the greater drouth there, with the result that only seedlings in the shade perish (Fig. 53).

Possibly some species grow best in sunny situations because they have high heat requirements. Others may escape destruction by fungi only under the low humidities that accompany bright light. Still others may require high light intensities to stimulate flowering, or to open the guard cells in order to obtain sufficient CO₂. In one study it was concluded that one of the most detrimental aspects of shade environment was the N deficiency brought about by a very slow rate of decay.²¹⁵ The fact that certain plants have much higher N requirements than others may account for their exclusion from shaded habitats.

The explanation of the superior growth of sciophytes in shade is just as complicated. In the first place sciophytes must have low light requirements.⁵¹ The compensation point for heliophytes may be as high as 4,200 L, but for shade plants it may be as low as 27 L.⁶³⁸ Deep-water algae and the algae and mosses that inhabit caves can

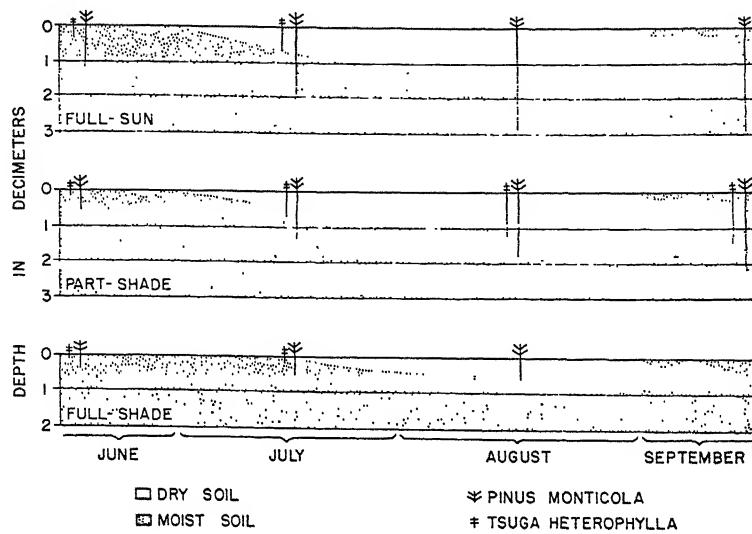


Fig. 53. Interrelationships among shading, root penetration, and progressive drying of the soil in northern Idaho. (After Haig, et al., 1941.) By studying the rate of root penetration of these two species in relation to the differing degrees of soil drought illustrated in Fig. 27, it is readily seen why both are permanently excluded from vegetation zones represented by profiles A, B, and C in that diagram.

grow under very weak light, often under intensities no greater than that of moonlight.^{63x} One investigator found that the sciophytes he studied differed from the heliophytes in possessing superior abilities to increase their chlorophyll contents under low light intensities.^{63y} Also it appears that others have concluded that sciophytes are plants producing their maxim leaf area in proportion to plant weight under shaded conditions, with heliophytes behaving the opposite.⁴⁵ As a rule, heliophytes can carry on photosynthesis more rapidly under full insolation than can sciophytes, and the latter are more efficient than the former under low light intensities (Fig. 54). However, if sun plants are made to grow in the shade for a time, their compensation points lower and they lose their ability to profit by full sunlight, therefore heliophytes and sciophytes are more critically defined on the basis of their usual habitats rather than by type of physiology.

Sciophytes may be at a disadvantage in full sunlight if they cannot manufacture chlorophyll at a rapid rate, for light continually decom-

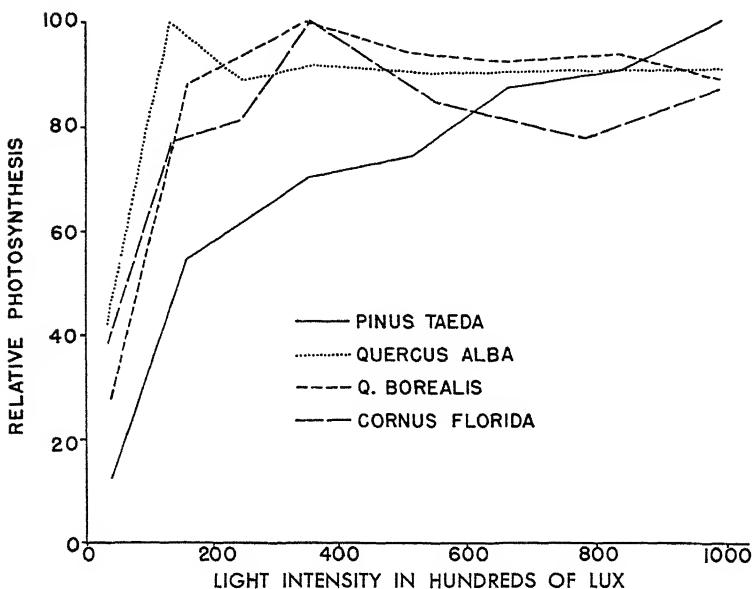


Fig. 54. Relative photosynthesis of tree seedlings expressed as percentages of maximum observed rates. *Pinus*, an obligate heliophyte, is relatively inefficient in weak light and assimilates most rapidly in bright light. Seedlings of all these species are dwarfed in the shade of a tree canopy, but this is regularly fatal only for *Pinus*.³⁶⁹ (After Kramer and Decker, 1944.)

poses chlorophyll, the plant remaining green only when it can maintain an equal rate of synthesis of these pigments. This effect of light is illustrated strikingly by *Selaginella serpens*, the intense green color of which fades noticeably during midday. Apparently the decrease in photosynthetic rate which is usually observed when a leaf is moved into bright light is due to rapid destruction of pigments, and the failure of sciophytes in sunny habitats may be due to this, at least in part.

Full sunlight is definitely supraoptimal in many instances where a physiologic explanation is obscure.⁴³⁷ In wheat it has been observed that bright light decreases the acidity of the cell sap and causes chlorosis which is believed due to pH interference with iron translocation.⁴⁰⁵ It has frequently been observed that when sciophytes are grown in full sunlight they develop an adverse internal water balance so quickly that the stomata close, thus causing photosynthesis almost

to cease. The possible effect of the conversion of light waves into heat waves upon the photosynthesis-respiration balance may also be critical.

Adaptations Minimizing Injury from Bright Light

Several characteristics of plants have been interpreted as beneficial in reducing injury from supraoptimal light intensities. In leaves exposed to bright sunlight the disc-shaped chloroplasts tend to become oriented against vertical walls so that only one edge is exposed to direct lighting. Possibly of similar significance are the vertically oriented leaf blades of such plants of sunny habitats as prickly lettuce (*Lactuca serriola*) and manzanita (*Arctostaphylos* spp.). In general heliophyte leaf blades are not flat and are not oriented at right angles to the path of incident rays as are those of sciophytes.

The decrease in chlorophyll content that accompanies bright light has its beneficial aspects, for it results in less light being absorbed and more transmitted, and the excess absorbed light would be converted into heat, which has a detrimental effect on the internal water balance and on the photosynthesis-respiration balance.

It has been observed in many plants that light intensity is directly correlated with the formation of anthocyanins, and these pigments, which are located in the superficial layers of cells, act as a reflective screen retarding the penetration of light into underlying tissue.²⁰ Red pigments reflect chiefly red rays, and, since long rays have the greater heating effect, their reflection greatly reduces danger from overheating. The temperature under red spots on fruit has been observed to be 22° C lower than under comparable green spots. The whitish surfaces of many heliophytes likewise provide as much protection against true light injury as against heat injury. The epidermis of shade plants transmits about 98% of the incident light, whereas the value for sun plants may be as low as 15%.

Motile algae are able to escape excessive illumination by vertical migration, and when the light is bright they are most abundant about a meter below a pond surface.

Light Relations in Plant Communities

In moist climates vegetation tends to be a complex series of superimposed layers, tall trees, low trees, shrubs, herbs, mosses, etc., and a high percentage of the flora are facultative or obligative sciophytes.

In dry climates the reverse is true, although even here there are many low plants that grow only in the shade of larger ones.⁶¹⁶

Among tall plants light requirements are of most importance in the seedling stages, for by the time they are mature the foliage occupies an elevated position and receives good lighting. Because the seedlings of different trees have different light and shade requirements (Table 11), some succeed only in habitats where others fail. Heliophytes frequently become established in the full sunlight of the original habitat. By consulting Table 11 it is easy to find an explanation of the fact that when abandoned fields in New England revert to forest the aggressive *Pinus strobus* is able to dominate the initial forest stand, but as shade develops conditions become favorable to the sciophytic *Tsuga canadensis*, *Fagus grandifolia*, and *Acer saccharum*, and eventually shade completely prevents new seedlings of *Pinus* from starting on the area. Likewise, mixed stands of *Pinus ponderosa* and *Pseudotsuga menziesii* always become pure stands of the more shade-tolerant tree within a few centuries. To return to the shade relationships of the New England trees, it should be noted that, although *Tsuga*, *Fagus*, and *Acer* have different light requirements, these differences are so small in relation to the heterogeneity of shade environment that all three commonly continue to inhabit an area together.

Most maples, beech, red oak, basswood, spruces, firs, yews, arborvitae, and hemlocks are obligative or facultative sciophytes, and most pines, soft maple, bur oak, willows, cottonwoods, aspens, tulip tree, birches, larches, and junipers are obligative or facultative heliophytes. Within these groups sun and shade requirements are of course far from uniform, and when other species are included there is a complete intergradation among them.

It must not be assumed that because shade-tolerant seedlings can live in dense shade they attain normal growth there. They are merely able to survive there for a long period as compared with others, thereby increasing their chances of benefiting from the death of an old tree that would leave a break in the forest canopy. Young trees have been known to persist in dense shade without making any diameter growth for as long as 46 years.⁶⁵³

Differences in seedling reactions to shade are exceedingly important in silviculture. Forestry in most parts of the world depends on the natural reproduction which follows the removal of each tree

crop, rather than on planting the desired species. Obviously the degree of completeness of logging is important because it determines the amount of sunlight available for the seedlings that will become established and provide the next timber crop. If shade-tolerant species are the more valuable, cutting must not as a rule be so heavy but that ample shade is left to encourage these species and discourage others. If light-demanding species are the more valuable, as they usually are, most of the timber should be felled at once, and sometimes it is desirable to burn the area lightly in addition in order to remove all shade. The problem of perpetuating light-demanding trees is a difficult one, for by the time a forest of these trees matures there is generally an understory of young shade-tolerant trees which, after the mature timber is harvested, tends to recover quickly from suppression and form a stand so dense that it completely prevents the reproduction of the desirable light-demanding species.

Underwater differences in cardinal light values are a very important factor governing the depth to which submerged plants can extend. Red algae as a group have lower light requirements than other algae. In the Puget Sound region this permits them to grow in the sea at depths of 25 m, whereas brown algae cannot synthesize carbohydrate below 15 m.⁶⁸² According to the well-known theory of complementary chromatic adaptation, the red pigments associated with the chlorophyll of the Rhodophyceae enable them to make exceptionally efficient use of the weak light, consisting mostly of short wavelengths, which reaches them. Supporting this theory is experimental evidence that red algae absorb a greater percentage of blue light than do either green or brown algae. There is considerable question, however, whether the nongreen pigments have much bearing on the ability of fresh-water aquatic plants to grow in deep water.¹⁷⁷

Attached algae grow as deep as 120 m in the exceptionally clear water of Crater Lake, Oregon, where they get less than 0.5% of sunlight. Vascular plants in fresh water usually extend no deeper than about 10 m even in the clearest lakes, and in shallower water the species form zones at different depths according to their light requirements. Only the lower limits of each of these zones seems to be directly by the amount of light penetrating the water; at the upper limits competition and shading effects become increasingly more important.

Transpiration

The detrimental effects of high light intensities include their influence in promoting rapid transpiration. Light stimulates the guard cells to open, as well as increases the permeability of the plasma membranes. From earlier discussions it will be recalled that the stomata of most plants remain open all day and close at night, and data were presented which showed that transpiration increases rapidly at daybreak and slows to a very low level at sundown, if not earlier, owing to a tissue water-deficit (Fig. 16).

Although sciophytes may use as much as 73% of the light energy available to them in the manufacture of sugar, heliophytes use only about 1% on account of the limitations of CO₂ supply, water deficit, etc. Of the remainder approximately one-third is reflected back from the leaf or is transmitted through it, and about two-thirds is absorbed, changed into heat energy, then lost by radiation or used up in the vaporization of water.⁶³⁸ Since some of the light rays that penetrate tissues are always changed into long heat rays, it is apparent that light effects can never be completely divorced from heat effects, and, because heat influences transpiration and other physiologic processes, the investigation of light as an ecologic factor is very complicated. As suggested earlier, heat effects can in part be ruled out by using aquatic plants as experimental materials, but there is no assurance that the results of such studies are directly applicable to land plants.

Many specific instances have been described in which the influence of shade in reducing transpiration as well as direct loss of water from the soil is decidedly beneficial from the standpoint of seedling survival.⁶⁰⁴ On the other hand there are many places where the moisture factor is most critical in the shade. The shade-induced dwarfness of seedling root systems results in either greater mortality under shade despite the milder intensity of soil drouth there (Fig. 54), or in the dense plant cover producing the shade offering seedlings too much competition for moisture and nutrients. In general, moisture conditions are more favorable under light shade than under dense shade or full sunlight, but, as emphasized earlier, shade implies a number of concomitant environmental conditions, and their net effect cannot easily be predicted.

Growth Form and Physiologic Characteristics

The amount of light available to a plant as it develops exerts a profound influence on the structure and functions of the organs finally produced. Light influences on structure of the shoots are essentially negative, for the blue and violet rays are the most important wavelengths governing differentiation, and their action can best be described as stunting.

In comparison to plants grown in the shade, individuals developing under full sunlight usually exhibit the following characteristics:

Morphologic Features

1. Thicker stems with well-developed xylem and supporting tissues.
^{510, 515, 535, 600, 708}
2. Shorter internodes.^{535, 708}
3. More prolific branching.⁸⁷
4. Smaller cells in leaf blades (in part a result of item 22 below), which in turn results in:
 - a. Usually smaller but thicker leaf blades or blade segments.^{96, 233, 258, 600, 708} Maximum blade area is usually attained under 20-50% illumination, but in certain species maximal cell size and area require full light.³¹⁷
 - b. Stomata smaller and closer together.^{283, 515}
 - c. Smaller vein islets.¹⁷⁵
 - d. More hairs per unit area, provided the leaves are pubescent.*
^{175, 233}
5. Walls of chlorenchyma cells in *Pinaceae* less folded.
6. Thicker cuticle and cell walls.^{96, 258, 283, 360} Because full sunlight tends to produce small blades of hard texture, tobacco grown for wrappers, as well as tea bushes, may be given shade to economic advantage.
7. Chloroplasts fewer and smaller.⁵⁴³
8. Better-developed palisade, which frequently occurs on both sides of the blade.^{96, 175, 258, 317, 360}
9. More weakly developed sponge mesophyll.
10. Smaller intercellular spaces.^{258, 360}
11. Greater ratio of internal/external leaf surface (largely a result of 4a above).
12. Lateral walls of epidermal cells less wavy.⁸⁷
13. Leaf blades not flat, less compound,⁷⁶⁶ and oriented at other than

* Leaf blades with a dense covering of hairs on the upper surface, as in *Verbascum thapsus*, resemble shade leaves anatomically even if grown in full sunlight.

right angles to the path of incident radiation^{96, 233} (Fig. 34).

14. Lower ratio of total leaf area to vascular tissue of the supporting stem.⁵¹⁵
15. Roots longer, more numerous and more branched, with a higher root/shoot ratio⁶⁰⁰ (Fig. 53).
16. Greater fresh weight and dry weight of both roots and shoots. A few plants attain maximum dry weight under less than full sunlight, and many show but a narrow margin of benefit with additional light above 50%.⁸⁷ The effect of a unit of light energy becomes more pronounced the nearer the approach to the limit of shade tolerance.⁴¹⁵
17. Larger and more numerous nodules on legume roots; better development of ectotrophic mycorrhizae.

Physiologic Features

18. Usually a lower chlorophyll content, with carotenoids consequently more apparent and the leaves greenish yellow.^{233, 543, 600}
19. Lower photosynthetic rate, when compared at moderate temperatures, for the photosynthetic rate of shade leaves is markedly depressed at high temperatures⁵²⁶ (related to items 10 and 18 above).
20. High respiration rate⁶⁷ and consequently high compensation point.⁶³⁸
21. Lower percentage of water on a dry-weight basis.^{258, 445, 600, 708}
22. More rapid transpiration^{258, 447, 515} (related to items 11 and 14 above).
23. Higher optimum fertility level.⁶⁰⁵
24. Higher salt content, sugar content, and osmotic pressure.^{360, 445} The protoplasts of shade leaves exert so little distending force against their cell walls that they wilt when their water content drops only 1-5%, whereas sun leaves can endure a loss of 20-30% without wilting.⁴⁵³
25. Decrease in pH of cell sap.^{405, 632}
26. High carbohydrate/N ratio.⁷⁰⁸
27. Low K content.^{465, 659}
28. Greater vigor of flowering and fruiting.^{87, 176, 233, 600, 708}
29. Earlier appearance of flowers^{233, 600} but later maturation of leaves.¹⁵
30. More calories per gram dry weight of seeds.⁴⁰⁹
31. Greater resistance to:
 - a. Temperature injury⁶⁸⁹ (related to items 4 and 24 above).
 - b. Drouth⁶⁰⁵ (related to items 4 and 6 above).
 - c. Parasites²⁷⁵ (related to item 6 above).

The morphologic differences described above not only characterize the same species grown under shade and under bright sunlight

but likewise tend to distinguish heliophytes from sciophytes when they are brought together in the same habitat. The two phenomena may be distinguished by the terms *helioplastic* and *heliomorphic*, respectively. However, it is to be noted that the parallelism between heliophytes and helioplastic modifications does not apply to physiologic characteristics to the same extent as to morphologic attributes. For example, heliophytes are capable of more efficient use of high light intensities than are sciophytes, whereas this relationship is reversed in helioplastic individuals, i.e., in series of individuals of a sciophyte grown under different light intensities, those in the denser shade make the more efficient use of light.¹⁶⁰

Because light sources usually emit heat as well as light rays, and because when light is absorbed it is converted into heat, the extent to which differences in structure and function associated with insolation are really results of heating and drying influences can never be determined with certainty. Certainly there is a remarkably close similarity between the helioplastic features enumerated above and xeroplastic features described earlier.

In addition to the usual differences in form between plants grown in sun and in shade, light intensity frequently affects the erectness of plants, but the nature of the influence is entirely unpredictable. In many species individuals grown in full sunlight are prostrate and those receiving shade grow erect.³⁷⁹ Reduced light stimulates bush lima beans to become climbing vines, whereas other species that are climbing vines under bright lights lose their power to twine when shaded.⁷⁰⁸

A green plant from which light is completely excluded responds somewhat differently from the reactions to suboptimal light discussed above. The stems become extremely long, leaves remain in an immature and unexpanded condition, and the plant loses its green chlorophyll pigments. A plant exhibiting such symptoms is said to be etiolated. Because etiolation improves the flavor and results in crisp tender tissues, plants such as celery and endive are usually covered to exclude light after reaching the proper stage of growth.

Germination ^{141, 189}

The seeds of most plants become sensitive to light when wetted. In certain instances germination is benefited; in others, it is retarded. *Verbascum thapsus*, *Lactuca sativa*, and *Paulownia tomentosa* will not germinate without light stimulation, and *Daucus carota*, *Rumex*

crispus, and *Picea abies* germinate better with exposure to light. In contrast, *Vanilla fragrans*, many *Liliaceae*, and *Primula spectabilis* require darkness, with *Bromus tectorum*, *Ulmus americana*, and many *Cucurbitaceae* germinating better in darkness.

The amount of light needed for stimulation is considerable for bluegrass (*Poa*), but for tobacco even 0.01-second exposure allows some germination.³⁴⁵ Seeds requiring light obviously must not be completely covered with soil when planted, but it has been found that, if seeds are soaked, given adequate light treatment, then dried again, light stimulation is retained and germination will take place even if the seeds are completely covered with soil.^{345, 670}

The physiologic explanation of light influence on germination is rendered especially obscure by the fact that so many other environmental factors influence the relationship.¹⁸⁹ For example, the light requirement of many kinds of seeds gradually becomes less important during dry storage.⁶⁷⁶ Also, a number of experiments have shown that the effect of light on seed germination can be reversed one way or another by temperature manipulation or by supplying oxygen, nitrates, or weak acids. These complex interrelationships have caused much confusion in the literature on this subject.

Reproduction

Earlier the fact was mentioned that insufficient light represses flowering and sometimes holds vascular plants indefinitely in the vegetative condition. Similarly the mycelia of many fungi grow well in darkness, but light is essential for the production of functional sporophores, and mosses growing in dimly lighted caves usually remain vegetative.

Because low light intensity favors vegetative development at the expense of flowering and fruiting, crops grown for vegetative parts are favored by climates with a high percentage of cloudiness, whereas fruits, grains, and seeds are favored by bright sun. The economic return on field and greenhouse crops is considerably influenced by the direction and degree of deviation from the seasonal norm of sunshine. Positive deviations in oceanic climates or during normally cloudy seasons are favorable, whereas negative deviations in the dry season of continental climates are beneficial. In regions where one or more seasons is cloudy, the lighting of a greenhouse during the cloudy season is a critical matter. The most benefit from sunlight is obtained when the greenhouse is oriented in an east-west direc-

tion, with the glass on the south side at such an angle that the sun's rays strike it at right angles when the sun is low in the sky.

Influence of Radiation on Nongreen Plants

For a long time it has been known that an exposure of bacteria to direct sunlight kills the cells. The lethal effect is due chiefly to the ultraviolet rays between 254 and 280 millimicrons, although violet and blue light have some effect. To a certain extent this knowledge has been put to practical use in sterilizing the air of public buildings with special ultraviolet lamps directed upward so as not to cause "sunburn" or "snow-blindness" of the occupants. In addition, ultraviolet irradiation has been used to sterilize drinking water and swimming pools, but the application here has been limited by the fact that these rays have very little penetrating power so that to be effective they must be played directly upon substances spread in thin films.

The same wavelengths that inactivate bacteria also have an inhibitory effect on fungi.⁶³¹ Very short exposures sometimes have stimulating effects, but long exposures are commonly lethal. When disease-producing fungi are more sensitive to ultraviolet than their hosts, irradiation can be used in controlling them. Thus certain powdery mildews of plants,²⁹⁰ as well as fungal infections in human skin, can be checked by irradiation.

Ultraviolet and light of short wavelengths also affect the growth form and pigmentation of fungi, and light has various effects on their reproduction. *Psalliota campestris* will fruit in either darkness or light, but certain other agarics will fruit only in the light. In some fungi light is necessary only to initiate the primordia of reproductive organs, but in *Pilobolus microsporus* the sporophores may be initiated in darkness but require light for development. In that fungus also spore discharge occurs only in the light.

Photoperiodism^{56, 719}

The length of the photoperiod * is of considerable importance to most plants,⁵⁵⁰ and their varied responses to this aspect of the light

* Actually it is the length of the dark period that is critical, but since the ecologist is concerned principally with natural conditions where the light and dark periods are reciprocally related, continued usage of the older terminology, based on a misinterpretation, is not too objectionable.

factor are designated by the term *photoperiodism*. Plants that develop normally only when the photoperiod is less than a critical maximum are called *short-day plants*, and those that demand a photoperiod in excess of a certain critical minimum are called *long-day plants*. The critical photoperiod varies with the species but usually lies between 12 and 14 hours for both short- and long-day plants. In certain plants the mature leaves receive the stimulus, in others the dormant buds, but in both cases the stimulus is transmitted to other parts of the plant by hormones.

Types of responses. Although a number of species are evidently not sensitive to this factor, the length of day determines for the majority whether the plants will produce flowers or remain vegetative indefinitely, and whether the internodes will be longer or shorter than normal.⁶ In short-day plants daylengths in excess of the critical period result in abnormally large vegetative parts (*giantism*) and suppression of flowering. Within the range of daylength short enough for these plants to flower, the shorter the photoperiod the shorter the life cycle. For example, in one series of experiments Biloxi soybeans flowered in 110 days under 12-hour photoperiods but required only 27 days under 5-hour photoperiods.²¹³

In long-day plants exposure to daylengths shorter than the critical period tends to shorten the internodes to the extent that the plant assumes a rosette form, and flowering is suppressed in addition.

In certain deciduous trees and shrubs, daylength controls leaf abscission and dormancy,^{213, 363} and in dioecious plants manipulation of the photoperiod may cause sex reversal.⁵⁸² Because maximum shoot growth is generally antithetic to flowering and maximum accumulation of food reserves, short-day onions and beets produce the largest storage organs under daylengths that are supraoptimal for the growth of the remainder of the plant. On the other hand long-day potatoes produce the best tubers when daylength is suboptimal for the aerial shoot.⁸⁷ In *Dahlia* storage organs are formed under short days and fibrous roots under long days, but it is interesting to note that the effect of daylength on root type is not related to the effect on flowering in the different varieties.⁷⁷² The relative size and anatomical structure of vegetative organs, degree of branching, lobing of leaves, hardening,⁶⁸⁹ susceptibility to parasites, pigmentation, germination,⁴⁵ nutrient requirements, and chemical composition⁷²⁴ may also be affected by the photoperiod.

In equatorial regions periodic behavior with respect to flowering

and dormancy is not strongly affected by seasonal changes in daylength. Many plants become active intermittently throughout the year whenever moisture and temperature are not limiting, and only a few respond to the slight seasonal differences in daylength.⁵⁵⁶

Species growing above a latitude of about 60° must be long-day (or indeterminate) plants because the brief growing season is entirely contained within that part of the year when days are longer than the critical period. Plants native to temperate latitudes may be adapted to either short or long photoperiods. Those that flower in early spring or late summer are mostly short-day plants; those that flower between these periods are mostly long-day plants.*

In a poleward direction the progressively shorter growing season and weaker light are more than compensated for by the increasingly longer photoperiod, so that assimilation accomplished during a day exceeds that of regions located at low latitudes.⁵⁰⁵ Therefore, considerable agriculture is possible in arctic regions if plants such as grains, berries, and tomatoes which either require or tolerate long days are selected. Timothy profits so much from the longer daily periods of photosynthesis that in a poleward direction its vegetative period is shortened and flowering is progressively earlier in relation to the beginning of the growing season.¹⁹¹

Photoperiodism and plant distribution. Light is an important factor in the local distribution of plants on account of the wide variation in intensity in different microenvironments, but the quantity and quality of light vary so little from one region to another that these aspects of light are not important factors in plant geography. The photoperiod, however, is of considerable geographic significance.

By the process of natural selection plants tend to become adjusted genetically so that they require daylengths corresponding to the region in which they grow and the season at which they come into flower. This adaptation is shown very well by the differences that may exist in photoperiod requirements of different segments of the population of a species which extends over wide range of latitude.^{192, 490} Such an adjustment to environment appears to be of negative value to the plant, for it reduces the plasticity without yielding apparent advantage.

* The flowering period is by no means always set by the photoperiod. Daffodils and other spring flowers are insensitive to daylength and come into flower as soon as temperatures are suitable; other plants such as Orange-flare *Cosmos* come into flower late in the season primarily because they require higher temperatures or a period long enough to develop flower buds.

A short-day plant that comes into flower after the summer solstice needs a long growing season, for it receives its photoperiodic stimulation long after the summer solstice. Because of the shortening of the growing season in a poleward direction, such a species finds a limit to migration where there is insufficient time between the arrival of suitably short days and the onset of winter for it to complete its seasonal development. Frost interferes with seed setting and injures tissues that are insufficiently hardened.^{6,8}

As a long-day plant extends its range in an equatorial direction, the first effect of decreasing latitude is to bring on the rest period prematurely. Still farther the plant finds a limit determined by the loss of the ability to flower.

Although those species that are indifferent to daylength are potentially cosmopolitan (as well as ever-bloomers), others cannot extend their ranges in either direction beyond the latitudes where they lose the advantage of efficient dissemination which usually depends upon flowering. Even among those species which possess highly satisfactory methods of vegetative reproduction, daylength may prove unsuited to the proper coordination between seasonal changes and the accumulation of adequate food reserves or may bring on other types of maladjustments.

Some practical applications. The importance of photoperiodism in relation to the artificial extension of the ranges of economic plants has two aspects. On the one hand photoperiodism may serve as a check upon the degree of north-south displacement possible. For example, beets change from the useful biennial habit to the useless annual habit at high latitudes. The fact has been well established that great longitudinal extension of crop plants is a failure, even when temperature is compensated for by altitude, unless new genetic stocks are developed.

On the other hand, abnormal photoperiodism may be desirable. The ornamental value of *Sedum telephium* is considerably enhanced by growing it below latitudes of 50° where daylength is too short for it to flower.⁶ In like manner, subtropical varieties of maize are grown in high latitudes when fodder is the desired crop. Finally, the classical example of making good use of abnormal behavior due to photoperiodism concerns Maryland Mammoth tobacco. This variety does not flower in the latitude of Maryland, and because of sterility and gigantism it produces fine crops of leaves at such latitudes, but other plants must be grown in the latitude of northern Florida

where the quality of the foliage is very low but where the plants flower vigorously and produce seed.

Plant breeders who desire to grow two or more generations of plants per year sometimes find it necessary to control light in order to bring about flowering and seed setting in the greenhouse in winter.²⁶² In the same manner interfertile varieties which have different flowering seasons can be made to bloom simultaneously, thus facilitating desirable crosses. Under certain combinations of species and market prices, floriculturists find it profitable to alter flowering seasons by altering daylength.³⁸²

Wherever it is economically feasible or experimentally desirable to supplement normal daylength to obtain certain desired results, good advantage can be taken of the fact that only very weak supplemental light, often less than 11 L, is adequate to produce the desired stimulation.⁷⁵⁷ Even bright moonlight (0.2 L) is strong enough to effect photoperiodic response in certain plants.

When plants are grown under distinctly short or distinctly long daylengths, the degree to which this factor controls structure and function is so absolute that it overshadows most minor genetic variation. For this reason plant breeders, in attempting to make selections with respect to adaptation to daylength, should grow their materials under near-critical daylengths, for this allows maximum expression of minor genetic differences.

LIGHT INFLUENCES AS MODIFIED BY TEMPERATURE AND OTHER FACTORS

Temperature and light influences are inextricably related in their influences on plants (Fig. 55). Suitable intensities of one compensate in part for deficiencies in the other. For example, photoperiodism can be altered somewhat by the intensity or quality of light, and it can be reversed by the manipulation of temperature.¹⁰ Thus, vernalization allows winter wheat to flower during long photoperiods, whereas without temperature stimulation these varieties are distinctly short-day plants.⁵⁴¹ Again, if moistened grains of sorghum and millet are kept in darkness for 5 to 10 days at temperatures between 27 and 29° C, the need for short photoperiods of the plants they produce is removed.⁴⁷

Possibly the efficiency of light energy increases with rising tem-

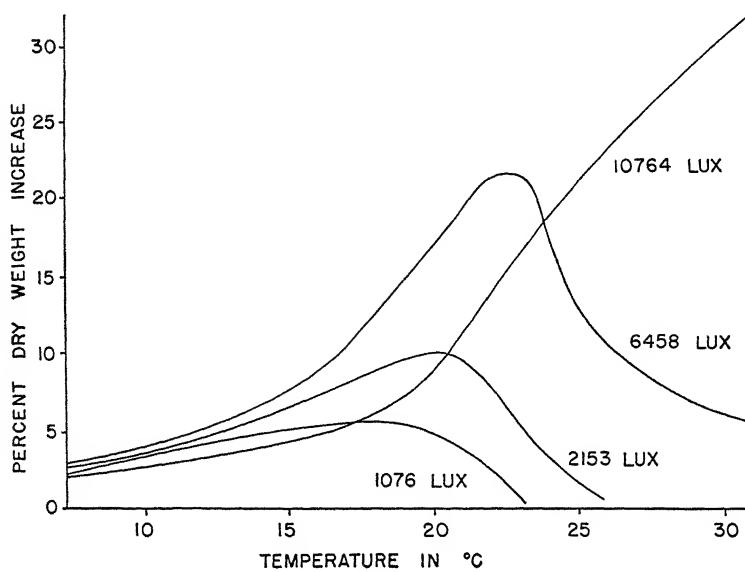


Fig. 55. Interrelations between temperature and light intensity, with respect to growth in young tomato plants. (After Bolas, 1934.⁸⁷)

perature. This is one explanation for the fact that in general the colder the climate the more intolerant a species is of shade.³⁸³ Nevertheless there is a strong likelihood that the controlling factor here is really the heating rather than the lighting effects of insolation. It is significant in this connection that at least certain plants exhibit the same structural characteristics when grown in shade at favorable temperatures as when grown in sun at lower temperatures.⁵¹⁰

When bacteria are exposed to ultraviolet radiation the lethal action of these wavelengths is increased either by a rise in temperature or a drop in pH. This fact and others mentioned above emphasize the point that, in experimental work with light, complete temperature records must be kept, for without them different experiments cannot be critically compared.

Finally, soil fertility is also known to affect light relations.⁶⁰⁸ The less fertile the soil, the lower the chlorophyll content of the leaves and the less their photosynthetic efficiency under a given amount of light. There are, however, definite limits to the extent to which fertility can compensate for inadequate light energy.⁶⁴⁶

LIGHT MEASUREMENT AND CONTROL

Light is even more difficult than temperature to measure or control. Since different wavelengths of energy have different physiologic effects, an ideal instrument for light measurement in ecologic work would be one which evaluated separately the energy values of different segments of the solar spectrum. It should likewise be portable, give readings directly, integrate direct with diffused light, and cover a range from at least 100 to 100,000 L. No such instrument has yet been placed on the market. All now available for ecologic field work have sensitivity curves which differ materially from the sensitiveness of plants and which change under different intensities of light or temperature.

Instruments for light measurement are designated as *photometers*, *illuminometers*, or simply *light meters*. Those that measure other forms of radiant energy in addition to light are most appropriately called *radiometers*.

Radiometers

The characteristic appearance of black objects results from their complete absorption of all visible wavelengths; whereas white and to a certain extent silvery surfaces reflect essentially all light. Owing to this difference in properties, black objects assume higher temperatures than white when both are subjected to equal illumination, and the difference in their temperatures is proportional to the intensity of illumination. A number of instruments utilize this principle. Since these are especially sensitive to infrared as well as to light, they must be employed in conjunction with a filter which cuts out infrared if the data are to be used as light measurements. A 1-cm layer of 0.1 N CuCl₂ is fairly satisfactory for this purpose.⁶¹ Instruments of this type usually have the disadvantage of lacking sensitivity under low light intensities, but the enclosure of the sensitive elements in an evacuated glass chamber overcomes the difficulty. Because photosynthesis is most strongly influenced by the longer wavelengths of light, and radiometers are more sensitive to the longer wavelengths, these instruments are best suited to light measurement where this function is being studied.

A simple radiometer may be made by sealing two thermometers in an evacuated glass tube, one with the bulb covered with flat black

paint, and the other with flat white or left naked. The instrument is kept in a dark box until a measurement is to be made; then it is removed and held in a horizontal position over the area where radiation is to be measured. The degree of difference registered by the two thermometers at the end of 5 minutes may serve as a measure of radiant energy, or the instrument may be calibrated against another type of instrument which expresses light in terms of luxes.³

A pair of spherical atmometers, one of which is black, can be mounted near each other and their evaporation rates compared.^{89, 401, 436, 641} These have been called *radioatmometers*. The members must be standardized to each other in the dark. Difference in water loss between black and white atmometers is closely related to pyrheliometer measurements (see below).²⁵¹

A third type of radiometer compares the degree of coiling and uncoiling of two flat metal spirals, one black and one white, which are fixed by their centers.⁷⁵⁹

Still another type of instrument in this category is the thermocouple, one junction of which can be attached to a black metal disc and the other to a reflective disc, the difference in heat absorption as indicated by the galvanometer being proportional to the incident radiation.⁶⁴ If a series of such thermocouples are connected so as to multiply this effect the instrument is called a *thermopile*. These instruments are rather expensive, but they yield instantaneous readings as well as continuous records and are considered by some the best type of instrument for general ecologic work.^{601, 602} There are many instruments of similar nature, such as the *pyrheliometer*, the *pyranometer*, and the *bolometer*, but they have been more widely used by meteorologists than by biologists.

Radiometers are the only light-measuring instruments that integrate all wavelengths of radiant energy. Each of the types to be mentioned below is sensitive chiefly to some particular segment of the solar spectrum.

Secchi Disc

The Secchi disc method is another ocular method based on the sensitivity of the eye; it is used to measure the penetration of light through water. A white disc about 20 cm in diameter is lowered horizontally during midday when the sky is clear until it just disappears from sight. This depth is recorded; then the disc is raised until it reappears and the depth is again recorded. The mean of

these readings is then taken as a measure of light penetration. Readings vary from about 59 m in clear ocean water to 1.5 cm in muddy rivers. The amount of error to be expected can be judged from the fact that the 2% illumination level in fresh-water lakes varies from about 1 m above to 1 m below the Secchi disc reading.⁴⁰¹

Photochemical Methods

When it is desirable to compare summations of light energy received over a long period, solutions that slowly decompose in the presence of light can be exposed continuously, then analyzed from time to time. The decomposition of oxalic acid in the presence of uranium acetate, and hydriotic acid in dilute sulfuric acid, have been used for this purpose.^{427, 560} A concentrated solution of anthracene in benzene slowly polymerizes when exposed to light, so that the amount of polymer accumulating during a few hours or days serves as an integrated expression of the light energy received.^{169a}

The degree of darkening of panchromatic film with standard exposure can also be used as a measure of light intensity, and through the use of filters the sensitivity can be controlled.^{352, 353}

Photoelectric Cells

Of all the types available for general ecologic work, no photometer yields absolute values of light intensities as quickly and conveniently as those employing photoelectric cells as sensitive units. These are portable, read directly, and when encased in a suitable water-tight cell can be used under water.^{90, 773} The technique is not without serious limitations, however. Both temperature and light intensity affect the sensitivities of the cells,³⁵² and it is not yet possible to get cells that are accurately standardized. Also, most types of cells are sensitive chiefly to the blue, violet, and ultraviolet rays. However, in measuring light with respect to its effect on structure and functions other than photosynthesis, this method is fairly satisfactory, for the shorter wavelengths to which the instruments are particularly sensitive are the chief ones involved.

Field Technique

From the above discussions it may be surmised that absolute measurements of light intensity using different instruments yield widely

discordant results. This problem can be considerably reduced where it is feasible to express light as a percentage of full insolation, for on this basis the differences among light meters are not so great.

Some investigators, in order to obtain a satisfactory value for average light intensity under vegetation, have directed the sensitive element of the light meter upward and placed it successively at equal intervals along a tape, taking an average of the readings made in the open at the beginning and end of the series as a basis of comparison. Obviously the day selected to obtain such measurements should be cloudless or, even better, uniformly overcast with the sun completely obscured during the entire series of measurements, and all measurements should be obtained in as short a period in midday as possible. The readings obtained under the plant canopy are best expressed in the form of a frequency curve.

When the sensitive surface of a light meter is flat, slight differences in the degree of divergence from a horizontal position yield widely different light values. To overcome this the sensitive surface can be mounted at the bottom of an opalescent integrating sphere.⁷¹⁷ Photoelectric cells are damaged ("solarized") by intense light; therefore it is always advisable to measure light as received through opalescent or ground glass, or as reflected from the surface of heavy white paper. The cells should also be protected from jarring as much as possible.

Light Control

In studying the effects of one factor it is always imperative that others be kept as nearly constant as possible, but the light factor is so complicated that this presents a very difficult problem in ecologic research. One investigator can seldom compare his experimental results with those obtained by another with the assurance that light conditions were essentially identical, and small differences in light conditions affect most plant functions.

Ordinary window glass screens out wavelengths shorter than about 330 millimicrons, so that special glass ("Vitaglass," etc.) must be used when it is desirable to grow plants under glass but exposed to complete radiation.⁷⁶² The ability of this glass to continue to transmit ultraviolet should be checked at intervals. To screen out other segments of the spectrum, colored glass filters can be obtained which transmit only certain definitely known ranges of wavelengths,⁵³⁵ but the intensities of transmission of such filters differ, a fact that pre-

sents no small problem in the use of such a series. Moreover, these glasses are very expensive.

The quantity of light may be increased by supplementary light from fluorescent lamps mounted under reflectors.⁷⁵⁶ These lamps are the most satisfactory because they give off relatively little heat as compared with the nitrogen-filled tungsten-filament lamp. The intensity of light can be controlled by varying the distance or the sizes or the numbers of lamps, and automatic switches can be installed to turn the lights on and off at any desired time. Although electric light has the advantage of being constant and reproducible, it is very different from sunlight, and therefore data obtained from plants grown under artificial light must be applied to natural conditions only with reservations.⁶⁰² Also it should be noted that light useful for photosynthesis must equal at least 11,000 L, and the brightest artificial light now obtainable with fluorescent lamps is of an intensity (*ca.* 27,000 L) that is too low for normal growth of obligative heliophytes. Furthermore, the bulky reflector of a fluorescent lamp is detrimental while the electricity is turned off, since the light most useful to a plant is that coming from directly above. By use of a dense bank of 300-watt reflector spot lamps, it is possible to obtain up to *ca.* 130,000 L beneath a 10-cm thick layer of running water that is necessary to remove objectionable heat.⁵³⁰

Different degrees of shading, starting with full sunlight, can be obtained by means of different numbers of layers of cheesecloth, muslin, or black sateen. Also, slat frames can be constructed in which different spacings of the slats allow different amounts of illumination to penetrate, or wire screening of different-sized mesh may be used. The screen and slat method has much to recommend it, since all wavelengths are affected equally. It has been widely used not only in out-of-doors experiments but also in providing suitable environment for the commercial growing of the sciophytic drug plant golden-seal (*Hydrastis canadensis*). If slats are used they should be narrow and well elevated, otherwise plant parts immediately beneath will be exposed alternately to periods of darkness and bright light. A cruder method of commercial light control is practiced in coffee plantations where the low coffee trees are grown under open stands of taller trees.

Wherever it is practicable, any method that makes use of natural sunlight which is reduced in intensity by slat frames, or is reduced in duration by transferring plants to a dark room, is the least objectionable physiologically as well as the least expensive.

CHAPTER SIX

The atmospheric factor

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From an ecologic standpoint the term atmosphere must include not only the thick gaseous envelope surrounding our planet but also the small and highly important masses of gas which penetrate or originate in the soil and in plant tissues.

An atmosphere is essential for life as we know it. In the first place, the atmospheric blanket surrounding the earth prevents such wide diurnal fluctuations in temperature as occur on other planets, fluctuations which would quickly extinguish all known forms of life. Second, there must be a continuous exchange of gases between an atmosphere and the living protoplasm of nearly all organisms.

The manifold effects of atmosphere on plants are in part direct, such as supplying CO₂ for photosynthesis and O₂ for respiration, and in part indirect, such as influencing the distribution of heat and light, and promoting transpiration, pollination, and dissemination.

METABOLIC ASPECTS

Composition of the Atmosphere

The principal gaseous constituents of the free atmosphere exist in fairly constant proportions by volume as follows:

N ₂ , approximately	79%
O ₂ , approximately	21%
CO ₂ , approximately	0.03%

Other constituents, the proportions of which vary greatly depending on time and place, are:

- Water vapors.
- Dust and smoke particles.
- Microorganisms (largely carried on dust particles).
- Pollen grains.
- Disseminules.
- Industrial gases.

Green plants increase the proportion of O₂ at the expense of CO₂ in the atmosphere. Although they continually produce CO₂ in respiration, whereas the release of O₂ in photosynthesis is limited to daylight hours and favorable seasons, the photosynthetic process is so much more vigorous than respiration that the net effect is to increase the percentage of O₂ in the atmosphere.

Animals and most nongreen plants always take in O₂ and liberate CO₂, so that their metabolism tends to offset the effect of green plants on the atmosphere. It is this complementary metabolism of animals and green plants that makes it possible to establish *balanced aquaria* which require almost no care. Indeed, if the balance is carefully adjusted, one of these biotic communities can be maintained in a stoppered bottle.

The CO₂ content of the air is also affected by the decomposition of carbonate rocks, by combustion, and by volcanic activity, all of which liberate this gas, and by the decomposition of feldspars, which absorbs it. Because the oceans have a great capacity for dissolved CO₂, carbonates, and bicarbonates, and at the same time present a great surface to the atmosphere, the constancy of the CO₂ content of the air seems in a large measure due to the influence of the oceans.

Judging from the lack of O₂ on other planets that have an atmosphere, and from the fact that geologic processes tend to use up O₂ but not to release it, we may assume that the photosynthetic process has been chiefly responsible for the accumulation and maintenance of O₂ in our atmosphere. Also, it seems reasonable to conclude that, since the percentage of O₂ appears to be remaining constant, an equilibrium has been established between the rate of photosynthesis and the rate of O₂ consumption by respiration plus geologic processes.

Exchange of Gases between Plant Shoots and the External Atmosphere

Gases enter vascular land plants by diffusing through the stomata and lenticels, then going into solution in the water contained in the

hydrated walls of the parenchyma cells, and finally diffusing through the walls and plasma membranes into the protoplasts. Waste gases of metabolism leave the plant by the same route in reverse. Because this system of gas exchange involves a wet cell surface that is in contact with the atmosphere, the loss of large quantities of water by evaporation is inevitable.

Not only does this mechanism prove hazardous at times from the standpoint of excessive transpiration, but gases contained in air that has been polluted by industries diffuse into leaf tissues and sometimes have toxic effects.

Atmospheric Pollution ^{439, 666, 895}

SO_2 from smelters hydrolyses in parenchyma to form H_2SO_3 . In dilute amounts this may be beneficial because the S is assimilated,⁴²⁶ but in high concentrations the plants may be severely injured by a destruction of chlorenchyma, with the leaves commonly assuming a water-soaked appearance followed by bleaching of intervenous areas. Often, before the development of modern methods of ore refining, almost all vegetation was killed in the vicinity of smelters (Fig. 56). In the refinement of aluminum or rock phosphate H_2F_2 is often liberated in quantities sufficient to devastate elements of the local vegetation, the symptoms being somewhat similar to SO_2 damage. In this case grazing animals may be indirectly injured.

Direct injury from SO_2 ^{19, 277} or H_2F_2 is likely to be confused with winter drouth injury.⁴⁷⁰ However, the latter affects only such woody plants as project above the snow cover, it cannot damage the foliage of deciduous plants, and is noticeably more severe on the windward sides of stands or isolated individuals. Also, winter drouth injury is sustained within a few days, and if the plant recovers, a slow return to normality is shown by the thickness of xylem layers, whereas poisonous gases only weaken the plant, gradually reducing annual wood formation until death.

Special types of atmospheric pollution are characteristic of large cities. Coal smoke produces soot, SO_2 , CO, and other noxious substances, whereas internal-combustion engines liberate vapors that react with ozone to produce injurious olefinic peroxidases, acids, and aldehydes. At times and places where there is moderate movement of air such pollution is objectionable chiefly on aesthetic grounds, but if there is no wind, and especially during foggy weather, the



Fig. 56. Area near Copper Hills, Georgia, where smelter fumes long ago killed all the plants of the original forest. Because high temperature and rainfall favor rapid erosion the year around, plants have not yet been able to revegetate the area since modern refining methods have come into use.

concentrations become serious for both plants and animals. The combination of fog with smoke is called *smog*.

In Los Angeles 1,000 to 2,000 tons of hydrocarbons derived from petroleum products may be released daily into the air, which is frequently foggy in winter. Mild smog injury to vascular plants causes a reduction in rate of growth, and with higher concentrations leaves take on a metallic sheen.

In London, where SO_2 from coal smoke is the most detrimental constituent of smog, a 4-day period of foggy weather caused at least 4,000 human deaths and much illness.⁶⁹⁵ Much economic loss was also sustained through the killing of flowers and foliage of glasshouse plants.

In general, the economic importance of smog on plants is small only because so few are grown in metropolitan districts, but the menace to dense human populations has attracted enough attention that much effort is being directed toward finding methods to cope with these atmospheric "open sewers." Epiphytic lichen floras on trees are often so affected by air pollution as to be useful indicators of its intensity.

Indirect detrimental effects of atmospheric pollutants on higher plants result from the action of their soluble products on soil organisms of decay and N fixation. Experimentally it has been shown that the influence of smoke on soils can reduce fertility enough to lower the protein content of timothy.¹⁴²

The CO₂ Cycle in Relation to Photosynthesis

The normal concentration of CO₂ in the free atmosphere is sub-optimal for photosynthesis, for glass-house experiments show that the rate of accumulation of carbon compounds can be materially increased by raising the CO₂ concentration to at least 20 times what is normal. However, high concentrations that are beneficial at first may prove toxic if sustained. Therefore, the atmospheric conditions under which an experiment is performed have considerable bearing on its significance in autecology.

The CO₂ cycle involves absorption by green plants from the air or water, fixation in photosynthesis, then eventually the oxidation of the organic compounds which returns the CO₂ to the air or water by one of three principal routes: (a) respiration by animals which have digested the plants producing the photosynthate, (b) respiration by animals which have digested the plant products, or (c) respiration by microorganisms which humify and mineralize organic matter. The CO₂ content of the air at any one time thus represents a dynamic equilibrium among a number of factors in time and space which affect the speed of various stages of this cycle.

At times when the photosynthetic process is very active, i.e., during the day and in warm moist weather, the concentration of CO₂ declines considerably below average, whereas at other times the reverse is true.¹⁰⁸ Obviously, determinations of the CO₂ content of the air with the purpose of showing the extent to which this factor is limiting photosynthesis should be made in late morning when photosynthesis is proceeding most rapidly. Also, sampling should take into account the vertical decrease in CO₂ content from the soil upward which results from absorption by the shoots, and from dissipation by wind currents of the supply of this gas that continually emanates from the soil. Great quantities of CO₂ diffuse from the soil at those times and places where the organisms have plenty of organic substrate and temperature and aeration are favorable for their activity. Measurements have shown as much as 20 pounds per acre per hour being liberated from soil.

In the lower layers of the atmosphere in a forest the CO₂ content may be nearly 6 times greater than the average concentration, and over moist, fertile soils in which microbial activity has been stimulated by cultivation the concentration may be 10 times normal. Soil organisms may liberate as much CO₂ per day as green vegetation uses up, thereby almost offsetting the usual tendency for a diurnal drop in CO₂ content and proving the importance of this source of carbon for low-growing plants. Herein lies an often unappreciated benefit derived from manuring soil, although excess stimulation of microbial activity may reverse the net benefit by creating supraoptimal concentrations of CO₂ in the soil itself. It has been pointed out that the high concentration of CO₂ near the soil in forests offers considerable compensation for the suboptimal light intensities there and may account for the greater efficiency of photosynthesis with respect to the supply of energy.

Because CO₂ is readily soluble in water, submersed plants that take this gas directly from the water have considerably more of it available to them in comparison with land plants. The absorption of dissolved CO₂ during daylight hours temporarily raises the pH of the aquatic environment during this time.

Factors Affecting Soil Aeration

In their respiration all soil organisms, including roots, absorb O₂ from and release CO₂ into the pore space of their medium. This results in a relatively high (up to 13%) concentration of CO₂ and a low concentration of O₂ in the soil, so that there is a steep diffusion gradient between the gases contained in the soil and those in the free atmosphere above. Gas moves through soil very slowly, however, so that CO₂ remains superabundant and O₂ deficient in most soils. Since the amount of gases and liquids in a soil are complementary to each other, the addition of a given volume of water displaces an equal volume of soil gases, and subsequently fresh air is drawn into the soil as the moisture drains away or is used up in evaporation and transpiration. Therefore the addition of water to a soil partly alleviates aeration conditions, provided the water drains out or is used up within reasonable time. Changes in temperature, barometric pressure, and wind velocity also contribute to the renewal of soil air, but diffusion is considered the most important single factor.³⁴ The CO₂ content of soil air tends to remain relatively constant, although the O₂ content fluctuates widely. Loams at field

capacity contain about 19% O₂ in the principal horizons of root activity, but rain brings about considerable reduction, even though it is temporary.¹⁰⁷ The degree to which the O₂ content of the soil air is depressed below that of the free air above depends on four major factors:

Rate of respiration of soil organisms and roots. Where soil organisms have an abundance of suitable substrate, and other factors are favorable, their activities alone keep the soil-oxygen concentration very low, and the CO₂ concentration quite high. In fact, variations in the rate of evolution of CO₂ from a soil are commonly used as a measure of variations in the rate of decomposition.⁷¹⁵ However, during the season of their active growth, the roots of plants may produce more CO₂ than the microorganisms.⁶⁸⁸

Amount of pore space. Heavy soils have more pore space than light soils, common values being 60% and 40% respectively, but the former tend to have a higher water content along with smaller pores, and both factors interfere with diffusion, thus bringing about relatively poor aeration. The swelling of colloids when heavy soils are wetted contributes further to their inferior aeration.

Porosity resulting from good aggregation or crumb structure, root channels, and animal burrows all increase aeration. Also, proper plowing greatly increases porosity temporarily in the plow sole; indeed one of the chief reasons for plowing is to provide a porous structure which will favor germination and seedling root growth. However, this benefit of plowing is gained at no little cost, for the same favorable aeration increases microbial activity to the extent that it becomes impossible to maintain a high organic content in cultivated fields. The equilibrium of organic content attained under cultivation is therefore lower than in virgin soils, the chief exception being that crop residues may raise the organic content of the upper horizons of forest soils that were low in the virgin state. Fallowing is most destructive to organic matter. Here good aeration is accompanied by higher temperature due to lack of shade, and by higher moisture due to lack of transpiration loss.

Another aspect of plowing that is important from the standpoint of structure and aeration is the timing of the operation in relation to soil moisture content. If plowing is done when the soil is at or a little below field capacity the structure is improved, but one plowing when the soil is too wet may destroy structure so completely that a decade of careful management may be needed to restore it.

Size of pores. The importance of pore size in aeration was illustrated strikingly by an experiment that showed a coarse sand with a total porosity of 55.5% to be 1,000 times more permeable to air than a fine sand with a pore volume of 37.9%. It can readily be seen that the permeability of the coarse sand is far out of proportion to the increase in total pore space and can be attributed only to some difference in the character, in this case the size, of the pores.

Pores so large that they will not hold water against the pull of gravity (except in the angles) remain filled with air almost all the time. These are the *noncapillary pores*. They are the most important from the standpoint of aeration because their aggregate volume represents the *minimal air capacity* of the soil, except for brief periods after a rain or an irrigation, and during such times these are the pores which allow gravitational water to percolate. Smaller pores, which remain occupied by water after a wetted soil has had time to drain, are called *capillary pores*. They are very important because they determine the maximum water a soil can retain, i.e., the field capacity.

High porosity is of no advantage if most of the pores are so small that they hold capillary water, for under such conditions the soil is essentially waterlogged at field capacity. Noncapillary porosity of 12% or less creates this unfavorable state. The roots of most upland plants will not penetrate horizons in such condition (Fig. 57); therefore the growth water they contain must be discounted.⁵⁹¹

An ideal soil should have high total porosity, which is about evenly

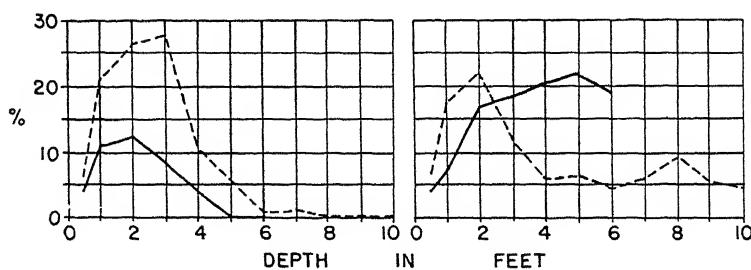


Fig. 57. Distribution of rootlets 2 mm or less in diameter (broken line), as related to the vertical distribution of noncapillary pore space (solid line), in two soils. (*Left*) A soil unfavorable for trees, with roots confined to shallow layer because of poor aeration below. (*Right*) A favorable soil with aeration permitting a more uniform distribution of roots. (After Schuster and Stephenson, 1940.)

divided between capillary and noncapillary pores.*³⁴ Sands generally have too little capillary porosity; clays tend to have too little noncapillary porosity.

Drainage. Regardless of the numbers and sizes of pores, if drainage is obstructed, the soil is poorly aerated because the pores remain filled with water that excludes air. The presence in a soil profile of blue-gray horizons, sometimes mottled with rusty brown, is a fairly reliable indicator of poor aeration caused by the rising of the water table to the top of that horizon for a considerable part of the year. The blue-gray color is due to reduced ferrous iron, and red or yellow color is limited to pockets or streaks of coarser material where ferric iron forms, these colors having rather reliable indicator significance for aeration in most soils.

As an example of the great importance of drainage in moist climates, on the Piedmont Plateau of southeastern North America the rate of height growth of pines bears a useful degree of correlation with the depth to the least-permeable soil horizon.¹³⁰

Effects of Suboptimal Aeration on Vascular Plants

Species differ widely with respect to their requirements for aeration. Many hydrophytes germinate and develop best under conditions that are inimical to the development of mesophytes and xerophytes.⁴⁰⁶ Manipulation of water tables has consequently proven useful as a means of eliminating undesirable plants. The responses of plants to suboptimal aeration vary considerably from one species and ecologic type to another and likewise with the degree of aeration. For certain plants there has been demonstrated an optimum degree of aeration above and below which plant functions are impaired.¹⁰⁶ The outline below indicates many of the types of responses to reduced aeration which have been reported in the literature; it also serves to show the considerable extent to which responses differ among species.

Morphologic Effects

1. Cell walls in roots remain abnormally thin.^{84, 406}
2. Root-hair formation is usually suppressed.^{150, 187}
3. Roots may be more numerous^{84, 729} or less numerous.¹⁵⁹

* Pore-space analysis is most conveniently made on small samples of undisturbed soil that are wetted and then subjected to standard moisture tension in the laboratory.³⁸⁷ Since the continuity of pores is almost as important as their total volume, infiltration rates may be of more significance than pore-space analysis.⁴⁹⁷

4. Root branching remains less complex.^{159, 406}
5. Dry weight of roots may be reduced or increased.²³⁶
6. Submersed organs may thicken as a result of formation of lacunar tissue⁶²⁰ or may become more slender thereby presenting much greater absorptive surface.⁷²⁹
7. Groups of stem cells may elongate radially to form conspicuous knobby swellings.⁴³⁴ This behavior represents physiologic disturbance, and is not adaptational as item 6.
8. Roots are shorter, and root systems occupy less space.^{84, 159, 406}
9. Root system becomes shallow, and sometimes root branches extend upward into the atmosphere.
10. Shoots occupy less space.^{84, 169}
11. Leaf area and number of chloroplasts may be reduced.²³⁶

Physiologic Effects

12. Roots change from aerobic to anaerobic respiration, at least in part, with a consequent accumulation of toxic by-products.
13. Permeability of plasma membranes decreases.
14. pH of plant sap declines.⁴⁰⁶
15. Rate of absorption of water and nutrients is reduced.⁴⁰⁶
16. Rate of transpiration is reduced (owing at least in part to item 15 above).
17. Rate of respiration is increased.¹¹⁰
18. Foliage becomes discolored.
19. Carbohydrate content may increase⁸⁴ or decrease.⁴⁰⁶
20. Reproductive processes are delayed or repressed.
21. Reproductive structures that have been initiated may absciss prematurely.⁴

Physiologic Aspects of Soil Aeration⁵²¹

Toxicity of carbon dioxide. Carbon dioxide becomes toxic when its concentration in the soil atmosphere rises to about 10%, and 30–50% becomes lethal. Under certain conditions, at least, the detrimental effects of excess CO₂ exceed those due to O₂ deficiency.^{105, 391}

Production of other toxins. Excess CO₂ and deficient O₂ favor the formation of H₂S and bicarbonates of ferrous iron and manganese, and these may increase to toxic concentrations. Normally roots secrete only H₂CO₃, but under conditions of deficient O₂ they may secrete formic, acetic, oxalic, and other toxic acids. Similar toxic products of metabolism are formed by microorganisms of decay forced to live under anaerobic conditions. Aeration inadequate for normal processes of decay is the primary cause for the accumulation of peat and muck, but the accumulation of toxins soon becomes a secondary factor of at least equal importance.

Unfavorable changes in the chemical states of nutrients.^{497, 710} The compounds of Ca, Mn, and Fe which exist under anaerobic conditions are not very available to plants, and nutrient deficiency results. Also S exists as sulfides rather than sulfates, and N as ammonium rather than nitrates. When the O₂ in a soil drops below the critical level certain bacteria begin to reduce nitrates to nitrites in order to obtain O₂, thereby further depleting the N fertility. Increase in CO₂ lowers pH, hence alters the availability of nearly all nutrients.

Deficiency of oxygen for root respiration and germination. The O₂ content of free air is always far enough above the minimal requirements of the shoots of terrestrial plants to be of no significance as an ecologic factor, but for seeds, roots, and soil-inhabiting organisms O₂ beneath the soil surface is usually suboptimal for metabolism. Some important microbes, especially *Clostridium*, have become so adjusted to life in media lacking O₂ that they remain inactive in environments where there are appreciable quantities of this gas, but most soil organisms are aerobes and must have at least a small amount of O₂ to respire. Likewise among higher plants certain hydrophytes have become so well adapted to waterlogged conditions that they grow better there than where the substratum is well drained.^{38, 729} Other plants native to wet habitats,³⁸⁹ as well as most mesophytes and xerophytes, are very adversely affected by a substratum that furnishes but little O₂. It has often been demonstrated that ordinary potted plants grow under conditions of suboptimal aeration even though the pots may be porous and the roots are most abundant at the surface of the soil next to the pot, for by forcing air up through the bottom of the pot growth is usually markedly stimulated. This problem of O₂ deficiency in the soil increases with rising temperature, for rising temperature increases the rate of respiration so that O₂ is used up more rapidly.⁹⁸

Roots usually do not begin to show definite injury until the O₂ content of the soil atmosphere drops as low as 5–10%.^{* 135} Ordinarily

* The ratio of reduced to oxidized substances in a soil affects its electric potential, hence by inserting electrodes into an undisturbed soil its *redox potential* can be determined. The measurements, symbolized by E_h , provide a graduated scale extending both up and down from a point at which reduction and oxidation are balanced. Although an excellent means of evaluating aeration, technical difficulties in method need to be resolved.^{504, 527} Other techniques for evaluating soil aeration involve measurement of (a) O₂ diffusion rate, or (b) rate at which O₂ is supplied to a porous absorber.³¹¹

the O₂ content of drained loams lies somewhere between this lower critical value of 10% and the 21% characteristic of free air, with the highest values nearest the soil surface. In general the roots of terrestrial plants are concentrated in the upper, better-aerated levels of the soil. In any position they are so nicely adjusted to the horizon in which they develop that disastrous effects frequently follow any disturbance of the aeration conditions, either by a rise in the water table or by the deposition of a smothering blanket of new soil upon the old surface (Fig. 58). When roots are suddenly deprived of soil O₂, absorption and transpiration decline strongly, leaves wilt and become

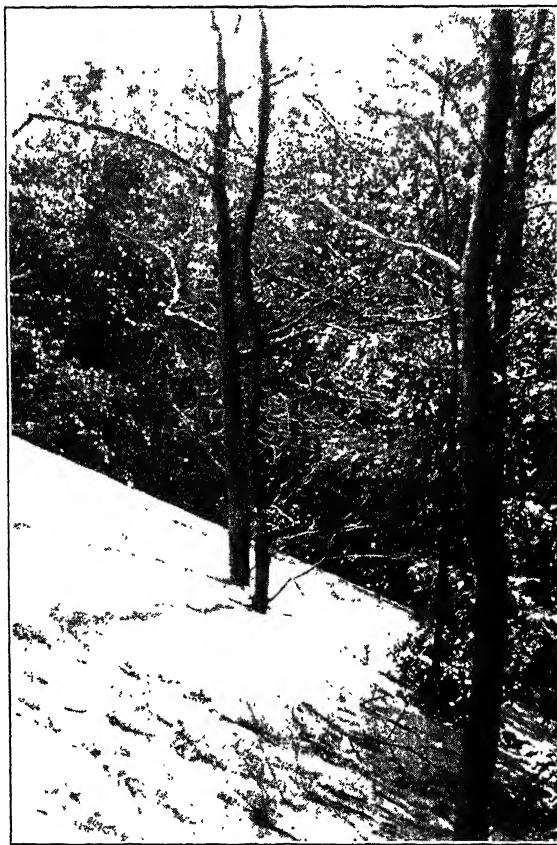


Fig. 58. Lee slope of a dune that is encroaching on a forest of *Quercus velutina* and killing the trees. Southern shore of Lake Michigan.



Fig. 59. *Tilia americana* showing adventitious roots that were formed during the period when the lower stem was covered by dune sand. An advancing dune usually kills trees that lack this ability to produce adventitious roots at successively higher levels.

discolored, and if conditions do not soon improve the plant dies.³⁸ These manifestations seem to result not only from a reduction in the roots' ability to absorb, but also from their inability to produce hormones necessary for the normal functioning of the shoots.⁷³⁵ Often, however, a decrease in degree of aeration is survived if the change is brought about so gradually that new roots have time to form and the distribution of absorbing rootlets becomes altered in accordance with the new conditions³¹⁸ (Fig. 59). When landscape engineers need to raise the ground level around a desirable tree, very coarse materials are used, at least for the lower part of the added layer.

Normal functions of most roots begin to be impaired as the O₂

content of soil drops below about 10%, and at 2% they can barely remain alive. Because the O₂ content of the soil drops abruptly to about 1% just above the water table, the roots of most land plants are restricted to soil horizons above this level (Fig. 60). Many can produce shallow root systems and thus survive where the water table is high;²³ but, where the root systems are thus altered to any great extent, the amount and vigor of shoot growth, fruit production, and longevity may be reduced.²⁴ On the other hand there are many plants such as *Typha*, *Scirpus*, *Salix*, and *Taxodium* which are unaffected by poor aeration and regularly send their roots well below the water table. Plants that can neither tolerate poor aeration nor develop a shallow root system are unable to grow where the water table is high.

The O₂ content of the waters of ponds and lakes is much higher than that of ground water but is still well below that required for



Fig. 60. Root system of *Populus trichocarpa*, which grew on a low river terrace until undercutting by the stream removed the supporting soil. Numerous secondary roots had penetrated vertically downward from the laterals, then ended abruptly in a series of short branches at a level which corresponded closely with the normal level of water in the river.

normal growth of most mesophytes. Along the margins of ponds, streams, and seas, various species show by their distribution their differing tolerances of high water tables, or of submergence during spring floods and high tides.³²⁵ Apparently the maximum depth of water coverage in submergence is less important than the duration of the interval when oxygen is unavailable to the roots. Some experimenters have found that a longer period of submergence is tolerated during the dormant than during the growing season, but in many cases water tables are high enough to be injurious only during the dormant season. The endurance of submergence at different seasons becomes a matter of considerable economic importance in cranberry culture where temporary flooding serves as a means of controlling insect pests.⁷¹⁴

It has often been noted that in rainy climates above-average rainfall is associated with reduced plant vigor and crop yield, but, since poor soil aeration is accompanied by reduced insolation, lower temperatures, and increased fungal parasitism, the relative importance of the aeration factor is not easily assessed. However, some influences of excessive soil moisture can easily be demonstrated by observing the effects of applications of a superabundance of water to lawns or crops. Under such treatment the roots of plants develop in the upper layers of the soil where aeration is best, thereby making them so vulnerable to drouth that the frequency of watering must be maintained. It is an important objective in irrigating to wet the soil only to the maximum depth to which the roots of the particular plants grown can be expected to penetrate. If irrigation is then suspended until growth water is nearly exhausted, roots obtain sufficient O₂ to extend to their maximum depth. Thus, the effective water storage capacity of the soil is at maximum, and the roots have access to nutrients in the largest possible volume of soil.

Attention was drawn earlier to the fact that, although roots do not elongate in the absence of growth water, root systems are most extensive where the moisture content approaches this critical minimum from time to time and the soil is never waterlogged. This is explained by the superior aeration of a soil when relatively little of the pore space is permanently occupied by water. Well-aerated soils in dry regions are a boon to deep-rooted plants, for they allow roots to penetrate to greater depths where the moisture supply is permanent (Fig. 61).

One of the conditions necessary for germination in most seeds is

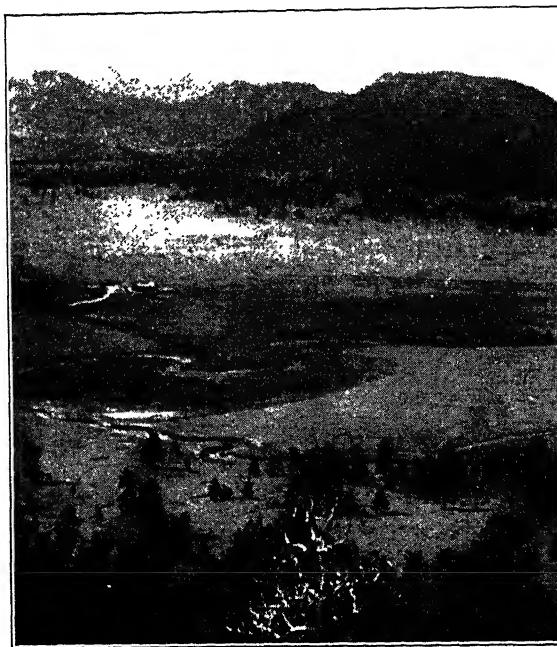


Fig. 61. Forest interrupted by the alluvial soils of an aggraded valley bottom. The coarse residual soils of the slopes favor trees because only a little water is required to raise the moisture content above the permanent wilting percentage, moisture penetrates rapidly below the reach of surface evaporation and shallow-rooted plants, and good aeration allows seedling roots to penetrate deeply and early. The heavy soils of the valley floor are occupied by xerophytic grasses which can endure protracted soil drouth, and which, on account of their relatively shallow roots, are favored by the high water-retaining capacity of the heavy soil. Estes Park, Colorado.

an abundance of O_2 . When this gas is deficient respiration proceeds very slowly and dormancy is prolonged, a fact that explains the longevity of seeds buried by plowing and earthworm activity, as well as the superior keeping quality of seeds stored in sealed containers. Buried seeds may remain viable without germinating for years but germinate promptly when brought back to the surface, this apparently holding true for lotus seeds buried in a Manchurian bog for 1,000 years. Although darkness may be an additional controlling factor with certain seeds, it is generally believed that a lack of sufficient O_2 prevents germination while the seeds lie buried.

Plant Adaptations to Suboptimal Aeration

Adaptations to suboptimal aeration may be morphologic, such as shallow root systems, special aerating tissues, and special aerating organs, or physiologic, such as low O₂ requirements and a special ability to respire anaerobically.

It has been pointed out that a special aerating tissue is not possessed by thallophytes, probably because they originated in water and have been thoroughly adjusted to the oxygen conditions there from the beginning,⁶²⁰ or because nearly all cells contain chlorophyll. Vascular hydrophytes, however, became so adjusted to the high oxygen content of the air that when they again take to the water they must make special provision for aeration. The meristematic tissue of land plants is at first lacking in intercellular air spaces, and it is significant that the growth of such tissue progresses slowly until the air-space system develops, at which time growth increases rapidly. Most vascular plants possess a continuous intercellular air-space system extending through their mature parenchymatous tissues and communicating with the external atmosphere by means of stomata and lenticels. In hydrophytic vascular plants these internal air passageways are elaborated as described earlier, and in certain mesophytes similar aerating tissues can be developed by individuals growing in wet soil or in water.^{33, 84} Submersed organs may not contain air channels if they are thin enough that nearly all cells are in direct contact with the water, or if the organs are located near the water surface where O₂ deficiency is least.⁹⁹

In a number of emergent hydrophytes, such as black mangrove (*Avicennia nitida*), special root branches grow erect until they project above the poorly aerated rooting medium (Fig. 62). These structures, called *pneumatophores*, usually have a well-developed intercellular system of air spaces continuous with the stomata so that they are of unquestioned value in gas exchange.⁴⁸⁸ Also, certain trees that grow on soil subjected to long periods of inundation produce excrescences that rise vertically from their lateral roots at points where the roots occasionally rise to the soil surface.^{245, 372, 516} They are typically cone-shaped but laterally flattened, and in North America they are commonly called *knees*. The possibility that knees are useful in permitting gas exchange between submerged roots and the free air is doubtful since (a) the only anatomical peculiarities of the xylem of which they are mainly composed is the prevalence of thin walls and parenchymatous elements, (b) the structures are frequently absent



Fig. 62. A young plant of *Rhizophora mangle*, a mangrove shrub, growing between tide levels in a muddy lagoon in Florida. The prop roots of this plant have lenticels that permit entry of O₂ into porous parenchyma extending downward. The pneumatophores of another mangrove shrub, *Avicennia nitida* (shoot not included in the photo), are shown projecting above the mud sufficiently to extend a short distance out of water at high tide.

where the water is deepest and aerating organs would be of most service, (c) the surfaces are covered with bark and frequently with mats of cryptogams and other epiphytic organisms as well, and these coverings would seriously interfere with gas exchange, and (d) experiments have shown that there is little gas exchange between knees and other roots.³⁶⁸

Bald cypress (*Taxodium distichum*) is a good example of a tree possessing these knees, and it is also peculiar for the enormous enlargement of the trunks at the water line (Fig. 63). It has been noted that at the water line a woody organ is kept wet by the constant lapping of waves yet has access to an abundance of O₂ not usually associated with such a wet condition. This special combination of environmental factors is closely associated with excessive cambial growth and seems to be the explanation for the production of both buttress patterns and knees.³⁷² Knees are produced only where the soil is periodically exposed to the air, and their height

growth depends on wetness and aeration to the extent that, although they may attain a height of 3 m, they never project above the highest level of wave action. Well-established bald cypress trees can endure partial submergence for periods of many years, but since seedlings are killed by submergence it is evident that stands owe their origin to periods of low water levels during which establishment is possible.¹⁶⁰

Many plants that grow best in muddy soils where the O₂ concentration is extremely low have developed especially low O₂ requirements for germination.¹⁶⁷ For example, the O₂ requirement for the satisfactory germination of rice is only one-fifth as great as that of wheat.³¹¹ In part this adaptation enables the embryo to respire anaerobically for at least a while. This type of adaptation is also necessary for certain upland legumes, the seed coats of which are relatively impermeable to O₂. Only after germination has progressed far enough to rupture the seed coat can normal aerobic respiration of the embryo begin.

The ability to respire anaerobically for a short time without injury



Fig. 63. *Taxodium* growing along the Wakulla River, Florida, showing the swollen bases of the stems and the spire-shaped "knees."

is possessed to a limited degree by the mature tissues of most plants, but it is especially well developed in certain hydrophytes which grow in still water or wet soil. Anaerobic respiration begins when the oxygen content of the intercellular spaces drops to about 3%, and it assumes increasingly greater importance, as indicated by alcohol production, as the O₂ content drops still lower.^{374,375} Possibly anaerobic respiration accounts for the ability of many anatomically unspecialized roots, such as those of willows, to extend into waterlogged soil.

Oxygen Deficiency in Aquatic Habitats

The photosynthetic activity of green hydrophytes may bring about a supersaturation of water with dissolved O₂ that often exceeds 500%. But in many aquatic habitats the amount of green vegetation is so small, or the conditions for photosynthesis are so unfavorable, that O₂ deficiency is very important. Oxygen readily dissolves into water where the surface is in contact with air, but subsequent diffusion of the dissolved gas is so slow that O₂ deficiency exists wherever there is a lack of convection to distribute it throughout the mass of water.

The O₂ contents of lakes and deep ponds are closely related to their thermal stratification, as described earlier.⁷³³ In summer the dense, cold water of the hypolimnion is immobile, with the result that the organisms that oxidize organic sediments keep its O₂ content almost zero. This is called *stagnation*. Wind friction causes a circulation of water in the epilimnion, the surface moving in harmony with the wind direction, and a reversed current flowing back through the lower epilimnion or thermocline. Thus in summer only the epilimnion tends to be saturated with oxygen, and consequently it is the principal region of biologic activity, although a few bacteria and other organisms live in the hypolimnion.

In spring and again in autumn there are transitional periods, when the direction of vertical gradient in temperature is reversing, during which there is no temperature stratification. At these times, the periods of *overturn*, convection currents set up by wind affect all water levels to the bottom of the lake, a condition which lasts the year round in very shallow bodies of water. All the decomposition products that have accumulated in the hypolimnion are dissipated during the overturns, and the entire body of water takes on the maximum and uniform load of dissolved O₂. Turbidity also increases as a result of current action on bottom sediments.

The hypolimnion again stagnates in winter, and, if an ice covering

prevents wind action on the water, hypolimnion conditions extend up to the surface.

Most organisms of decay require O₂ to be active, and when abundant substrate is available they use up O₂ at a rapid rate. Thus the release of sewage into streams reduces oxygen and depresses the populations of all organisms except those that decompose the material, but before the sewage is carried far the effect of turbulence in mixing oxygen from the surface has permitted nearly complete mineralization of the organic compounds, and the resultant high fertility of the waters allows plant and animal life to flourish in great abundance. In the absence of pollution, organisms of the natural biota are fewer but are more evenly distributed along the stream course.⁷¹ Controlled biologic disposal of sewage is accomplished in a very short time by artificial aeration in receiving tanks, so that streams, even at the point where they receive the resultant effluent, are spared the effects of extremely low O₂ content.

WIND

Wind is an ecologic factor of considerable importance, especially on flat plains, along seacoasts, and at high altitudes in mountains. It affects plants directly by increasing transpiration, by causing various kinds of mechanical damage, and by scattering pollen and disseminules. Less direct effects are numerous, including the transportation of hot and cold masses of air, moving clouds and fog that change water relations and alter lighting conditions, modifying temperature on shores to lee of bodies of water, mixing air and thus preventing temperature inversions, etc. Some of these aspects of wind influence have been discussed previously; others remain to be considered.

The rate of movement of air is generally expressed as average velocity over an interval of time, such as an hour or month, but, since the flow of air is not nearly as constant as the flow of water in a stream, mean velocities for long intervals of time are very misleading. Wind of gale proportions may blow for a few minutes yet not be suspected from the magnitude of the hourly total.

The velocity of wind is affected by the configuration of topography and vegetation masses, by position with respect to seashores, by major paths of wind movement, and by regions of calms. Also the rate of air movement increases regularly with increasing height above the

ground, a fact that must always be taken into account in collecting and interpreting records.

Wind is usually measured⁴⁶² with a Robinson *anemometer* consisting of a series of three or four horizontally rotating arms terminated by cups. The arms are fixed to a vertical shaft which operates a train of gears motivating a dial. If dial readings are used, only average velocities can be computed for the interval between readings, but electrical recording apparatus can be attached which records the time required for each mile of wind to pass, and this provides a much more accurate index of velocities. In microclimatology a hot-wire anemometer is often useful.⁴⁹⁸

Where the significance of wind lies in its effect in increasing transpiration, evaporation measurements are more useful than separate measurements of wind and saturation deficit because of the difficulty of evaluating separate environmental factors. Also, in interpreting wind measurements, it should be remembered that wind velocity at a particular level in the open is always lower than the velocities on all but the leeward side of the canopy of an isolated plant.

Windbreaks ³⁴⁹

Even a cover of low herbaceous plants strongly reduces the velocity of wind along the ground, and forest cover, especially where the canopies of individual trees are staggered at different heights, reduces the velocity by as much as 80%. By means of this action in slowing down wind currents near the earth's surface, plant cover prevents wind erosion of the soil and causes winds carrying particles to drop their loads. The accumulation of dune sand and loess is thus promoted by plants.

Special plantations of trees or shrubs are often made with a view to providing protection against wind for fields, orchards, buildings, or livestock. A *windbreak* or *shelterbelt* is a densely planted strip of tall vegetation, usually between 50 and 200 feet wide, oriented at right angles to the direction of prevailing winds in order to reduce their velocity near the ground.

The effect of a natural grove of trees or of a windbreak, especially one flanked by shrubs, may extend to the leeward for a distance 100 times the height of the trees. However, at this distance the influence is never more than barely detectable, and significant benefits do not extend more than about one-fifth of this distance. By deflecting currents upward there is also produced an effect in a windward direc-

tion which may be detected up to about seven times the height of the trees. If windbreaks are spaced at about 25 heights they provide continuous though variable protection.

Obviously the effectiveness of a windbreak depends on the denseness of the vegetation, open stands having very little retarding influence on strong winds. When the plantations consist of deciduous trees the effectiveness is considerably reduced during the leafless season, so that theoretically it is best to use evergreens where suitable species are available. Wind velocity itself also has something to do with the effectiveness of a windbreak, for the percentage reduction in velocity varies under different wind conditions.

Five major classes of benefits can be expected from windbreaks: (a) a reduction of evaporation and transpiration, and consequently a more efficient use of soil moisture and less severe winter drouth injury; (b) a reduction of damage by breakage, lodging, and abrasion; (c) a reduction in the movement of soil by wind; (d) a more even distribution of snow over undulating topography; and (e) a saving of as much as 40% in the heating of dwellings.

Other influences of windbreaks are detrimental, so that the plantings must be made judiciously in order to accentuate the beneficial aspects and minimize the following detrimental influences.³²

Windbreak plants exhaust the soil of moisture and nutrients, and they cast shade in their immediate vicinity, thereby considerably reducing the total crop area. With some trees root competition may be evident for a distance greater than twice the height of the tree, but usually roots do not cause much damage beyond the spread of the crown. Root-competition losses are minimized by: (a) using species that tend to root deeply, (b) promoting deep rooting by breaking up subsoil hardpans with dynamite before planting the trees, (c) cultivating deeply near the trees to prevent the development of long shallow laterals, (d) growing highly competitive crops near the trees during the period of their establishment, (e) avoiding the use of species that spread by suckering, (f) planting the windbreaks as narrow as is feasible and spaced as far apart as is consistent with the desired results, and (g) using part of the space adjacent to the trees as a lane.

The economic loss due to shading can be offset to a certain extent by using trees that produce narrow crowns, and by growing adjacent to the windbreak strips of special crops that do not demand much direct light, especially hay crops where flowering is not essential. If rows of trees are planted along every stream, outcropping, and

roadside, a relatively small amount of the arable land will have to be relegated to windbreaks. Also, maximum effectiveness demands narrow, long, continuous rows of trees with shrubs.

Very dense windbreaks may promote snow drifting to the extent that moisture derived from snow is reduced in the fields and increased in the vicinity of the windbreak where only the trees can benefit much from it. In some instances drifting is so extreme that the water table is actually raised for a time after the spring thaw. This influence can be counteracted to some extent by leaving the windbreak as open as possible near the ground level.

Finally, windbreaks interfere with breezes which would otherwise keep the air stirred up and at a more uniform temperature; thus they tend to increase temperature extremes in their vicinity. Although this increases the frost hazard, the high midday temperatures hasten the ripening of grain. Soil temperatures are also affected by windbreaks, but it is not so easy to classify these effects as beneficial or detrimental.

The net effect of well-planned windbreaks is definitely to increase total crop production, although this statement applies chiefly to arid and semiarid regions and seacoasts, and for seasons that are not extremely dry. The balance is thrown still further in a favorable direction when the species used for windbreak planting have some value as a source of food and cover for game animals, or as fence-posts or fuel.

Wind Influences on Plants

Desiccation. In still air evaporation is simply a process of diffusion, but when air is in motion the process becomes strongly affected by convection. Wind causes evaporation even when the saturation deficit is zero.

With plane surfaces, the rate of evaporation increases with the square root of wind velocity. Thus, while breezes have a strong influence, the influence is not proportionately greater at high velocities. Herein lies the explanation for the practice of whirling a psychrometer. Evaporation from the wet bulb is affected very little by wind velocities in excess of 5 miles per hour, and the instrument can be conveniently rotated by hand at about 10 miles per hour. Therefore, if rotation is rapid, wet-bulb depression is effected almost entirely by relative humidity.

Wind increases transpiration by removing layers of humid air

which tend to accumulate adjacent to the plant surfaces, and this action is especially facilitated by small-sized leaf blades. Wind also bends leaves, causing alternate expansion and contraction of the inter-cellular space, which forces saturated air out and draws drier air in. The efficiency of the cuticle becomes a very important factor in determining a plant's resistance to wind desiccation, for at high velocities the tissues lose turgidity so that the guard cells close, and thereafter almost all transpiration is cuticular.²²⁰

Previous mention has been made of the physiologic consequence of wind in increasing the evaporative power of the air during cold weather when both the water-supplying power of the soil and the permeability of the protoplasm are low. In certain mountainous regions, such as the east slope of the northern and central Rockies, *chinook* or *foehn* winds are especially injurious in this respect. These are warm, dry winds that make their appearance suddenly, raising the evaporative power of the air before the soil has had opportunity to warm up, so that the ability of woody plants to maintain a satisfactory internal water balance is severely taxed.²²⁵

Even when the weather is warm and the soil moderately moist, the protracted influence of dry winds can kill leaves and twigs and can



Fig. 64. *Arenaria sajanensis*, a typical cushion plant of high, windswept ridges in the central Rockies.

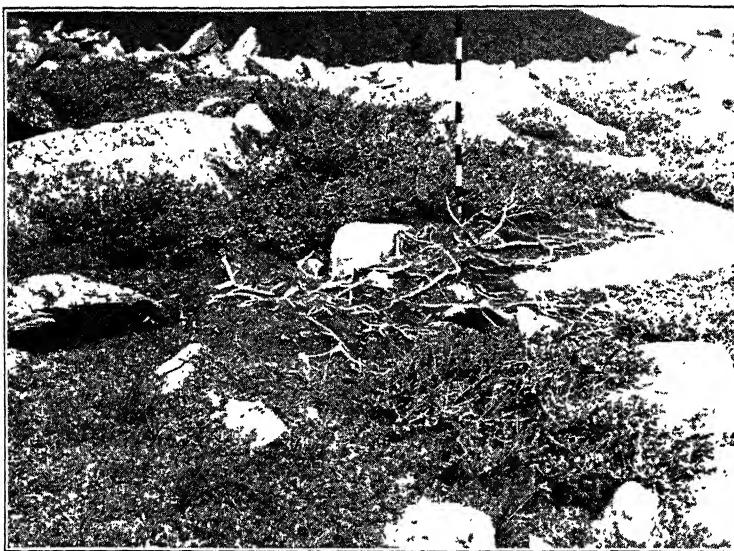


Fig. 65. *Picea mariana* growing at upper timberline near the summit of Mt. Katahdin, Maine. These trees are at least a century old, and, though still sterile, are about as large and as old as the habitat will permit. Dwarfing and deformation by winter desiccation are illustrated. Meter stick is marked off in decimeters.

injure fruits or cause them to be abscised.⁵⁵³ The taller the plant the more subject it is to desiccation, as well as to other forms of wind injury. Some plants, normally tall and erect, become low and spreading as a result of wind action. Others are normally low of form and thereby escape much wind damage. The most efficient life form on windy habitats, and one which is especially prevalent there, is that of the *cushion plants* in which streamlined contours are presented by the uniform tips of numerous crowded branches (Fig. 64). The action of wind on many erect plants molds their shoot systems into this cushion form (Fig. 65). When branch tips are killed, the lateral buds produce vigorous growth so that each dead terminal is replaced by several shoots of lateral origin. The resultant complex system of branching gives the shoots of one plant or of a small group of plants a dense streamlined contour. Wind injury to the terminals occurs frequently enough to perpetuate these contours. Each time the twigs that have elongated the most vigorously are killed back the farthest (Frontispiece).

Dwarfing. Plants developing under the influence of drying winds never attain a degree of hydration, and consequently of turgidity, that enables them to expand their maturing cells to normal sizes. As a result all organs are dwarfed, without necessarily being deformed, because constituent cells become fixed at subnormal sizes. Obviously dwarfing attributable to wind can result only from those winds that blow during the period when cells are expanding and maturing.

At the approach to a seacoast, or arctic or alpine timberline, or the edge of a forest that is adjacent to an extensive prairie, the stature of the trees is gradually reduced, and the farthest outposts are usually confined to those parts of the topography that afford the most protection from wind. Here the dwarfing is due to an unfavorable internal water balance, and the confinement of individuals to protected areas is usually due to death by desiccation of seedlings that germinate on exposed places. Trees may be so dwarfed that specimens a century old are no larger than a small shrub (Fig. 65).

Dwarfing involves low dry-matter production, yet the total water utilization is not reduced in proportion, so that the transpiration efficiency is reduced if not halved.^{140, 516} In addition the date of maturity is advanced in some plants, and the number of secondary branches may be increased.¹⁹⁷



Fig. 66. *Pinus flexilis* at upper timberline on Long's Peak, Colorado. Wind pressure has caused the tree to develop in a prostrate position from the beginning. Blasting ice particles have eroded the bark from a large area at the base of the trunk.



Fig. 67. Wind-trained *Pinus ponderosa* and *Quercus garryana* along the Columbia River gorge in Oregon. In *Pinus* strong and persistent wind pressure has bent the branches on the windward side around until they point permanently in a leeward direction. Toward the base of the canopy secondary growth has deeply buried the curved bases of these branches. (Photograph by courtesy of D. B. Lawrence.)

Deformation (wind-training). When developing shoots are subjected to strong wind pressure from a constant direction, the form and position of the shoot may become permanently altered (Fig. 66). Deformation is not necessarily accompanied by dwarfing, for moist winds can mold the form of a shoot without appreciably reducing its size. Trees with inclined trunks are commonly observed on ridges, in prairie groves, and along coasts where exposure to unidirectional winds is common and severe.

Trees vary greatly in their response to the force of strong wind.

Limber pine, black spruce, certain live oaks, etc., often grow flattened against the ground while other trees in the same habitat remain erect, although they show other types of wind influence. Tree branches often develop only in a leeward direction. Sometimes this is due entirely to pressure effect as is shown by the fact that branches emerging from the windward side of the trunk remain alive but are all strongly and permanently bent around until they are pointing in a leeward direction (Fig. 67).³⁸⁴ In other instances asymmetrical crowns result from the death of all buds that form or twigs that emerge on the windward surface, as a result of desiccation, erosion, or breakage.

Constant winds that cause a woody plant to sway chiefly in one direction evoke an adaptational response in many plants consisting of a flattening of the trunk, roots, and branches in a plane parallel to the direction of flection.^{223, 320} Thus the organs assume a plank shape and in *Cupressus macrocarpa* along the California coast some trunk sections may be over six times as long as broad, the growth rings showing that the cambium has been active chiefly on the leeward side of the stem (Fig. 68). Here, as well as in other types of asym-



Fig. 68. *Cupressus macrocarpa* on the coast of California, showing the effects of landward winds. Growth rings tend to be extremely thin except on the lee sides of the stems so that the trunk and branches become strongly flattened in a direction parallel to the wind.

metrical ring formation, the thickest rings are associated with that side of the bole with the most foliage and hence the greatest photosynthetic capacity. Because wind deformation lessens the value of timber, reforestation or afforestation near windy coasts often necessitates the establishment of a special shelterbelt of trees to prevent deformation which would reduce the marketability of the main plantation.

Anatomical modifications. When a tree bole becomes inclined from wind deformation or landslide, a dense, reddish type of xylem called *compression wood* forms on the compressed side and tends to offset further bending in this direction. This anatomical modification also occurs on the windward side of trees that show no outward symptoms of wind influence.⁶⁴⁰

In herbaceous plants wind-sway may stimulate the formation of more collenchyma than usual.⁷⁰⁵

Lodging. Lodging is the name given a form of wind injury sustained especially by grasses, such as wheat, maize, and sugar cane. Wind frequently flattens these plants against the ground, but, if the stems are not too mature, the prostrated plants become partially erect once more by means of differential growth at the lower nodes which remain meristematic. Such injury is never important except where some factor promotes rapid growth and soft tissues, and it is important only in crop plants. Under mechanized farming, much wheat can be lost by lodging so late in the season that the stems cannot become erect again and the inflorescence remains too low to be picked up by harvesting machinery. Even when lodging takes place early enough that the stems can regain erectness, the crop may suffer because of mechanical injuries sustained by the stem tissues.

Lodging as well as breakage, to be discussed below, is due to unusually violent winds, especially the tornadoes of temperate regions and the cyclonic typhoons or hurricanes of tropical regions.

Breakage. The susceptibility of plants to breakage by wind (Fig. 69) depends somewhat on the type of anatomical structure and on whether or not the tissues are frozen. Trees such as cottonwoods and river maple have soft, brittle wood and are especially susceptible to breakage. Basswood has equally soft wood but is considerably less susceptible because of the strong sheath of phloem fibers surrounding the wood. The brittleness of any twig is increased greatly when it is frozen, and buffeting at this time may cause severe pruning.

The severity of breakage is also magnified by glaze storms³⁸⁴ or



Fig. 69. Breakage and uprooting by the 1938 hurricane, on Mt. Washington, New Hampshire. During the hurricane wind velocity exceeded 160 miles per hour on the summit of this mountain.

wet snows, both of which leave the branches bent to the limit of flection by a heavy burden of solid precipitation. Also, trunks weakened by disease, or fire scars at the base, break easily.

Trees may be uprooted even if the stems successfully resist breakage by high winds. Single trees or groups of trees which are uprooted in a forest are often referred to as wind throws or windfalls. This type of damage, which involves breakage of at least the smaller roots, is favored by anatomical structure that does not resist much tensile force and by shallow rooting. Sometimes artificial drainage channels are dug when a forest is partially cut, with a view to promoting deep rooting and thereby reducing wind throw among the residual trees.

The conditions under which a tree develops has a very important bearing on wind throw. Trees grown in dense stands, and thus not exposed to full wind velocity as they grow, lack the stimulus to become sturdy which open-grown specimens have. When one or two trees are blown over in a wind storm the ones left standing around the edge of the opening are very vulnerable to the next strong wind,

and in this way an area of wind throw may increase in size for some time. Trees that are blown only until they lean permanently soon lose much of their value as lumber because compression wood forms on the lower side and the bole becomes elliptic in cross section.

When a forest is logged a few trees are often left to supply seed for the next generation. Foresters have tried leaving these seed trees in groups for mutual protection against wind throw. However, this procedure is usually not very effective. Wind throw among such seed trees is almost as great where the groups are subject to mild winds as where winds are strong, showing the universal weakness of trees developing under forest conditions.⁷⁸¹

The root system of a wind-thrown tree usually lifts a disc of soil which subsequently falls in a heap at one side of the basinlike depression from which it was removed. In this way the surface of the mineral soil over a forest is kept from being flat, and small mounds of mineral soil free of organic layers are made available for the establishment of those species which cannot get started on organic layers. The unevenness of the mineral surface results in very uneven accumulations of organic matter, for such material fills in the depressions before accumulating over the small knolls.

Abrasion. When wind carries particles of ice or soil it is a very potent abrasive force. Bark and buds may be eroded away from the windward sides of woody stems when the plants are situated in exposed places. This abrasive action is strongest a few centimeters above the ground or snow, and frequently it results in an evident cutting zone on woody plants (Frontispiece, Fig. 66). Crops grown on sandy soils in windy climates are often damaged in this way.

Effects of erosion and deposition. An undisturbed plant cover is very effective in preventing the movement of soil by wind, but when even at one point the cover is thinned or destroyed, wind may scour out the soil so as to expose the roots of the adjacent living plants, bring about their death, and thereby increase the area of devastation (Fig. 70).

The eroded material likewise becomes a hazard to the existence of plants in other places where it is deposited, for few species can tolerate the sharp reduction in aeration about their roots that follows the deposition of new soil upon the old. Those that can survive this change develop adventitious roots at successively higher levels on the stem as deposition takes place.

Salt spray.^{61, 492} Along seacoasts the spray that dashes into the air in the breakers is carried ashore by wind, and in the immediate

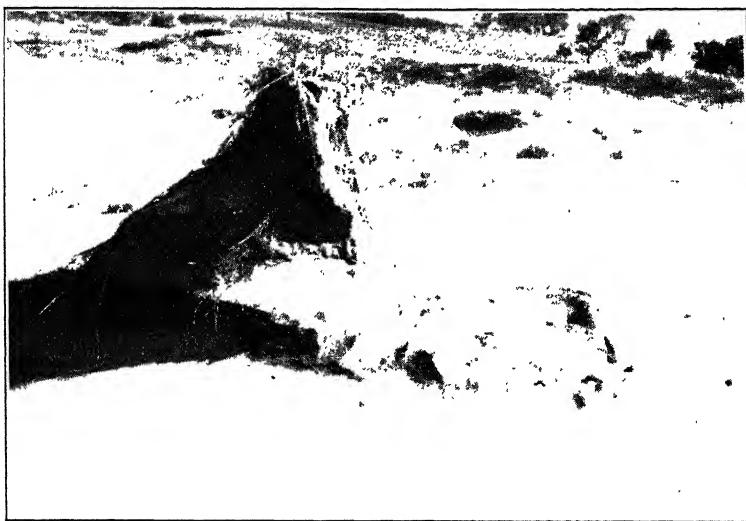


Fig. 70. An area where wind erosion of sand has destroyed by undermining all the original vegetation except one bunch of grass which has held intact the soil encompassed by its root system. Central Minnesota.

vicinity of the ocean wind-borne salt spray may have considerable injurious effect on certain sensitive species of plants (Fig. 71). By means of special salt traps it has been shown that the quantity of air-borne salt diminishes with increasing distance from shore, and by spraying plants it has been demonstrated that species differ in their tolerance of salt, the most tolerant generally growing nearest the sea.⁴⁹¹ Plants sensitive to salt spray can grow near the ocean only if they are sufficiently short-lived to complete their life cycles between storms when most of the spray is deposited. Salt damage from severe storms has been observed as far as 45 miles inland.⁴⁷²

The chief damage seems to follow those storms that are not accompanied by rain, so that as the salt spray dries it leaves a film of salt on the plant surfaces. The exact manner in which this film causes injury is not known, but the withdrawal of guttated water back into leaves may well bring into them hypertonic solutions formed while the extruded droplets were in contact with the incrustation on the cuticle.¹⁴⁶

Two chief methods of reducing salt-spray injury to economic plants are available. By planting a windbreak of salt-tolerant species



Fig. 71. Shrubs streamlined by winds blowing from the right off the ocean at Roosevelt Beach, Oregon. Probably wind desiccation and salt spray are both important here.

along the ocean, much of the spray is combed out of the wind.⁶¹⁹ Second, the toxic effects of salt on the soil can be reduced through the application of potassium salts which have an antagonistic effect on the sodium ions.

Snow cover. In areas of uneven topography, snow is swept from the windward slopes of the prominences and deposited on lee slopes and in hollows. Winter after winter the same areas remain thinly covered, while others near by accumulate excessive drifts and are covered for longer periods. The boundaries between vegetation types on habitats where accumulation is scanty and those where it is excessive are often very sharp. Woody plants may be excluded from habitats lacking a protective snow cover, they may be regularly killed back to the snow surface where accumulation is moderate, or they may again be excluded from areas where deep drifts accumulate and persist far into the normal growing season. This wind transfer of snow frequently produces very dry soils along the top of a sharp ridge oriented to get maximum exposure.⁶²⁷ The direct measurement of precipitation here is not only difficult, but snow transfer after

falling makes the measurements rather meaningless from the stand-point of plant ecology.

On level topography the irregular drifting of snow has great effect on the thermal characters of environment. When the same series of habitats are compared over a series of years the temperature relations are occasionally reversed simply by the vagaries of snow drifting.

Wind Pollination (Anemophily)

The most primitive pollen-producing plants are believed to have depended on wind to transfer their pollen from anther to stigma. In cool and cold climates the vast majority of trees, shrubs, and herbs are still wind pollinated. When atmospheric turbulence carries pollen to considerable altitude it may be transported several hundred miles.

Although air currents are omnipresent, this method of pollination has certain inherent disadvantages. Because of indiscriminate scattering by wind, the chances of any one pollen grain's alighting on the proper kind of stigmatic surface at the opportune time are very remote. Therefore great quantities of pollen must be cast on the wind if the chances of pollination are to be increased to a point where an adequate seed crop is assured. In consequence wind pollination is very wasteful, as is shown by the sulfurlike films of pollen that form on the soil and water surface when conifers are pollinating, and by the abundance of pollen in the air which so frequently causes hay-fever in man. Nevertheless anemophily has proved quite successful, for many of the plants that dominate the earth's vegetation are wind pollinated, especially the Coniferae, the Glumiflorae, and the Ameni-tiferae.

Anemophilous plants have developed certain morphologic adaptations that facilitate wind pollination. The flowers have underdeveloped perianths, but long stamens which are extruded and which sift their pollen into the passing breezes, and stigmas that are well exposed and often feathery, with the result that they literally comb pollen out of the wind. The flowers are typically unisexual, and they are located high on the shoot where they are never shielded from free air movements by the foliage. The pollen has a smooth exine that is not adhesive so that the pollen readily falls from the anther sacs as they open. In certain gymnosperms the buoyancy of the pollen grains is increased by a pair of attached air bladders which greatly increase the frictional surface without adding much weight.

Wind Dissemination (Anemochory)

Wind is the most efficient agent of dissemination, and most terrestrial plants depend on it to scatter their disseminules. Among these plants (called *anemochores*) there are recognized six common types of adaptation which tend to facilitate wind dispersal.

Minute disseminules.⁷⁶⁰ The seeds of the Orchidaceae, Ericaceae, Orobanchaceae, and a few other higher plants are very small, some weighing no more than 0.002 mg. Because of their small sizes, such seeds, together with spores, bacterial cells, etc., are readily picked up and carried by wind. The fact that viable spores are abundant in the upper atmosphere as high as 2 miles may account for the widespread distribution of most fungi and algae and many mosses. The rapid spread of the fungi causing chestnut blight and blister rust of white pines after they were introduced into North America furnishes adequate proof of the efficiency of this type of disseminule.

Comose disseminules. The friction surface of many disseminules is greatly increased by the production of hairs which do not materially increase the weight. The disseminules of the Salicaceae, Asclepiadaceae, many Compositae, *Clematis*, *Epilobium*, etc., all possess sufficient fuzziness so that they are readily picked up and carried by wind. A velocity of 2 miles per hour will keep dandelion achenes afloat, so that this type of disseminule can be blown many hundreds of miles over land or sea.⁶²⁵ Experiments indicate that comose disseminules may be more buoyant than the most minute glabrous types.

Winged disseminules. Many seeds (*Catalpa*, *Betula*, Pinaceae) and one-seeded fruits (*Ulmus*, *Acer*, *Fraxinus*) produced by trees possess a wing that greatly retards the speed of descent of these structures when they are cast. This allows the wind to carry the disseminule a considerable distance to the leeward of the tree before it strikes the ground. The taller the tree and the slower the descent of the disseminule, the more effective a given wind velocity.⁶²² Studies with seed traps of the lateral distribution of seeds of *Pseudotsuga menziesii* in Oregon have shown that an abundance of seed can be expected to fall as far as 900 feet from the trees,⁵¹⁵ but updrafts and strong winds can carry seeds of this type for a distance of several miles.

Saccate disseminules. In *Physalis*, *Ostrya*, and many Chenopodiaceae the seed is enclosed in an inflated papery structure which can be rolled over the ground or snow surface by wind.

Tumbling disseminules. The entire aerial shoot of *Salsola pestifer*, *Cycloloma atriplicifolia*, as well as the isodiametric and finely divided inflorescence of *Panicum capillare* and the globular fruiting bodies of certain puffballs (*Bovista*, *Disciceda*), break off from the remainder of the plant when mature, and as the structures are rolled along before the wind seeds or spores are knocked loose from time to time. This type of disseminule is common only in grassland or desert vegetation.

The catapult mechanism. Incompletely dehiscent dried fruits, which remain in a vertical position at the stem tips when they mature, often retain seeds that are shaken out only a few at a time when buffeted by wind. Examples are provided by *Delphinium*, *Iris*, *Oenothera*, and *Papaver*.

In these plants the disseminule itself is in no way modified, but the mechanism functions as a catapult which develops small but effective centrifugal force. Obviously this mechanism is not very efficient for covering distance rapidly.

The direction of dissemination when wind is the agent is strongly influenced by the degree to which the winds blow from a constant direction. If winds are unidirectional most of the disseminules will be carried in that direction, and the only chance for plants to migrate in the opposite direction is provided by occasional eddies. It is significant that in forests anemochory is most prevalent among the trees, and relatively uncommon among the undergrowth plants that live in a microclimate with little wind movement.

CHAPTER SEVEN

The biotic factor

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The average green plant is commonly referred to, or at least thought of, as an "independent" organism, in contrast to other plants and animals that cannot synthesize their own food. In reality, however, not even green plants are independent, for they are considerably influenced by other organisms, although in ways that may not be obvious. For example, the blueberries and huckleberries (*Vaccinium* spp.) depend on nectarivorous insects for pollination, upon fructivorous birds and mammals for dissemination, and, like many other green plants, they depend in part on fungi associated with their roots to absorb nutrients.

Even the CO₂ used by a green plant in photosynthesis has been released in respiration by other organisms, and the oxygen used in respiration has been accumulated largely by previous generations of green plants. The amounts of heat, light, moisture, and nutrients available to one plant are all conditioned by the proximity of other plants, and most of the soil nitrogen, it will be recalled, is organic. Furthermore, at least some injury from disease-producing organisms and herbivores is sustained by almost all plants. Our "independent" plant, on analysis, therefore turns out to be no more than a figment of the imagination, and it becomes clear that the environment of any organism is always in part biologic as well as physical.²⁶¹ In fact, certain biologists have been so impressed by the omnipotence of the biologic factor as to deny the existence of autecology. Technically they are correct, but for practical purposes the separate environmental factors should be studied in relation to the individual, as far as possible, before communities as such can be studied intelligently.

Physical factors are usually the true governing forces of environment, one organism ordinarily affecting others by its ability to modify the physical environment; the numerous means of doing so have been pointed out in many places previously. However, some biotic influences are truly direct, as illustrated by grazing, animal pollination, and animal dissemination.

CLASSIFICATION OF SYMBIOTIC PHENOMENA

The terminology concerning the relationships of one organism to another has long been in a state of confusion. In one proposal aimed at clarification, interrelationships between two organisms are thought of as involving a "stronger" and a "weaker" partner:²⁷⁰

Effect on Stronger Partner	Effect on Weaker Partner		
	Damaged	Unaffected	Benefited
Benefited	Predation	Allotrophy	Symbiosis
Unaffected	Amensalism	Neutrality	Commensalism
Damaged	Synnecrosis	Allolimy	Parasitism

Even though this system provides a clear distinction among some common and often loosely used terms (predation, symbiosis, commensalism, parasitism), it adds an equal number of new terms. Furthermore, in antibiosis it is often difficult to decide which is the stronger of the two partners. Also, *Salmonella typhosa* is stronger than man at the onset of illness, but man soon overpowers the microbe, thus classification of the relationship is reversed as the disease runs its course. Finally, shade of a tree may affect an herb without its being possible to classify the influence as benefit or damage.

Another classification reduces the emphasis on special terms,⁴³² and at the same time uses the word symbiosis (Gr. *syn* = together, *bios* = life) as intended by De Barry when he proposed it in 1879. Each of the examples of the categories given below is located in the position that seems most tenable in the light of existing information, but it is very likely that further research may necessitate a re-evaluation of certain relationships:

- I. *Disjunctive symbiosis* (i.e., associated organisms not in constant contact).
 - A. *Social* (i.e., no direct nutritional relationships).
Includes the effects of one plant on another with respect to shade, air movement, soil moisture, etc.; also the substrate relations of saprophytic organisms.
 - B. *Nutritive*.
 1. *Antagonistic*.
Herbivorous animals and their food plants; carnivorous plants and their prey.
 2. *Reciprocal* (Reciprocal here does not imply that the two symbionts are mutually helpful, but rather a condition of reciprocal parasitism in which the advantages of the relationship exceed the disadvantages for both organisms).
Animals effecting pollination or dissemination incidental to their activities in obtaining food from plants; fungi cultured and disseminated by insects that use them for food;^{601, 700} the agricultural pursuits of man; ants inhabit-

ing hollow thorns or other organs of vascular plants which they defend against the attacks of other insects.⁶⁹¹

II. *Conjunctive symbiosis* (i.e., dissimilar organisms living in contact with each other).

A. *Social.*

Lianas and epiphytes using other plants for support; algae inhabiting the hollow interiors of *Azolla* leaves, the roots of cycads, the ventral cavities of the thallus of *Anthoceros*, the stem cortex of *Gunnera*, the surface layers of the hair of sloths, etc.

B. *Nutritive.*

1. *Antagonistic.*

Parasitism of plants by bacteria, fungi, Protozoa, nematodes, insects,¹⁹⁴ mistletoe, etc.; parasitism of animals by bacteria and fungi.

2. *Reciprocal.*

Lichens; mycorrhizae; nitrogen-fixing bacteria in roots, stems, and leaves; algae inhabiting Protozoa, coelenterates, molluscs, flatworms, the egg membranes of amphibians, etc.^{85,}
²²²

HERBIVOROUS ANIMALS

Grazing and Browsing *

Many ecologic problems are involved in the management of natural or artificial types of plant cover so as to provide good forage for livestock and game animals.⁶⁵¹ First there is the matter of food preferences. For each kind of animal, the plants available to it may be classified in a sequence from those that are very palatable to those that are strictly avoided. Palatable species tend to be the most severely injured, and unpalatable ones may escape injury and even be benefited by the release from competition. Among the palatable species differences in nutritive value must be taken into account in those planting and management practices that benefit certain species at the expense of others.¹¹⁶ Owing to differences in seasonal development different types of plant cover may have different periods during which they are grazed to best advantage.⁵⁷⁶

* *Grazing* refers to the use of unharvested herbs as forage by animals; *browsing* refers to a similar use of shrubs or trees, although there is not much significance to this distinction.

Grazing may injure a plant either because the frequency or degree of removal of its photosynthetic organs curtails its assimilation or because of its susceptibility to trampling. Less direct but even more important consequences of intense grazing result from erosion and deposition that result when plant cover is so thinned that the soil is no longer protected from the erosive influences of wind and water. Grazing damage to certain species is magnified by drouth cycles, the plants being unable to cope successfully with such a combination of adverse conditions. On the other hand, plants the shoots of which are kept clipped to small size by continual grazing may be better able to withstand drouth. They do not keep the moisture reserves depleted to the normal extent, and furthermore, during the drouth the smaller plants make correspondingly smaller demands on the supply of moisture stored in the soil.

The effects of grazing on different species of plants depend to a large extent on life form. Annuals that are palatable quickly disappear from an area if grazed so much that they cannot set many seeds. Among herbaceous perennials, palatable grasses and sedges withstand grazing much better than forbs, for on account of their basal meristems the leaves are not destroyed when only distal segments are removed; in fact the plants are stimulated by mild grazing. Also, trampling is least apt to injure the vegetative buds of these plants, for they do not extend above the ground surface and are protected by the dense tufts of foliage. Shrubs are less easily injured by browsing than herbs are by grazing because browsing, generally confined to new growth, removes but a small portion of the shoot, and because the greater longevity of shrubs increases the chances of survival of sufficient seedlings to replace old-age mortality. Low shrubs may be kept reduced to dwarf "hedged" mats, and tall shrubs and trees, if they can attain a height above the reach of animals, finally become essentially free from direct injury.

The least damage is sustained by perennials if the new foliage is not removed until the plant has had sufficient time to restore part of the underground food reserves which were nearly exhausted in building up the new photosynthetic organs (Fig. 72). If grazed heavily and early the plant is weakened and killed because the roots are starved and consequently become inefficient in performing their normal functions. By practicing deferred rotation grazing, different parts of an area are grazed at different seasons, and from year to year the seasonal sequence is altered.⁶⁵¹ This allows each unit to be relieved from grazing pressure every few years at the season most

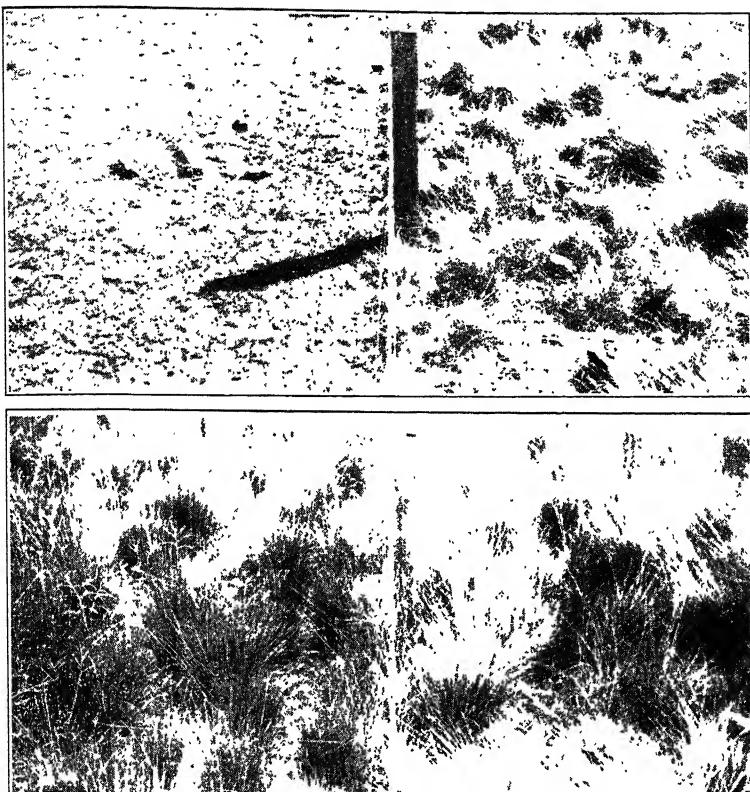


Fig. 72. (Upper) Late winter picture showing completeness of utilization of *Agropyron spicatum* in the pasture to the left of the fence. (Lower) Later picture of the same area showing that the close utilization of cured forage during the dormant season had no significantly detrimental effect on subsequent growth. The bunches in the ungrazed area to the right are denser and lighter in color owing to the presence of old bleached shoots. *Sisymbrium altissimum*, an annual forb which has been favored by cattle grazing, is conspicuous in the grazed area. Southeastern Washington.

critical for seedling establishment and the restoration of depleted food reserves.

The aspect of vegetation may be markedly changed as a result of these differences in reaction of individual species to the grazing factor. Grazing in shrubby vegetation often increases the numbers and sizes of the shrubs by removing the competitive grasses that

would otherwise use up a large share of the water and nutrients available. Grazing in purely herbaceous vegetation generally results in a sparser plant cover consisting of fewer species, these being unpalatable or having such a short growing season that livestock does not have time to cause serious damage. The kind of animal that produces most of the grazing influence is also an important factor. Sheep normally prefer forbs, horses and cattle prefer grasses, and goats and deer prefer broad-leaved woody plants.

Although rodents are much smaller than the principal livestock animals, their numbers are often so great that they exert an important degree of grazing pressure. Even mice can keep vegetation in a depauperate condition. Each family among the burrowing rodents affects but a limited area about its burrow, but if communal, large areas may be nearly denuded. The jack rabbit, in contrast, depends on speed rather than a burrow for safety, and therefore affects wide areas rather uniformly. In southern Arizona 22-55% of the forage potentially available for livestock may be utilized by the worthless jack rabbits.⁶⁴² Perhaps nowhere else has rodent damage been so devastating as in Australia, where rabbits were introduced for sporting purposes and have increased in vast numbers.⁶⁴³

The grazing and browsing of certain wild rodents of positive economic importance are not wholly detrimental. In heavily populated areas the value of cottontail rabbits as game has stimulated considerable effort in creating and preserving vegetative conditions favorable to this animal. Also the beaver, valued for both fur and erosion control, deserves to have those species of trees the bark of which forms the bulk of its diet planted and conserved.

Animal Destruction of Seeds and Seedlings

The high energy value of the particular types of foods stored in seeds makes them very satisfactory as a source of food for animals. Insects, birds, squirrels, mice, and other rodents annually consume tremendous quantities of seed.^{102, 630, 663} The amount of seed produced by a particular type of plant varies considerably from year to year, and, when the crop is small, seed-eating animals may destroy it entirely. As with grazing animals, the factor of food preference enters strongly here. Small seeds may be neglected when larger ones are available.³⁹

Reforestation has often been tried by scattering seed over the

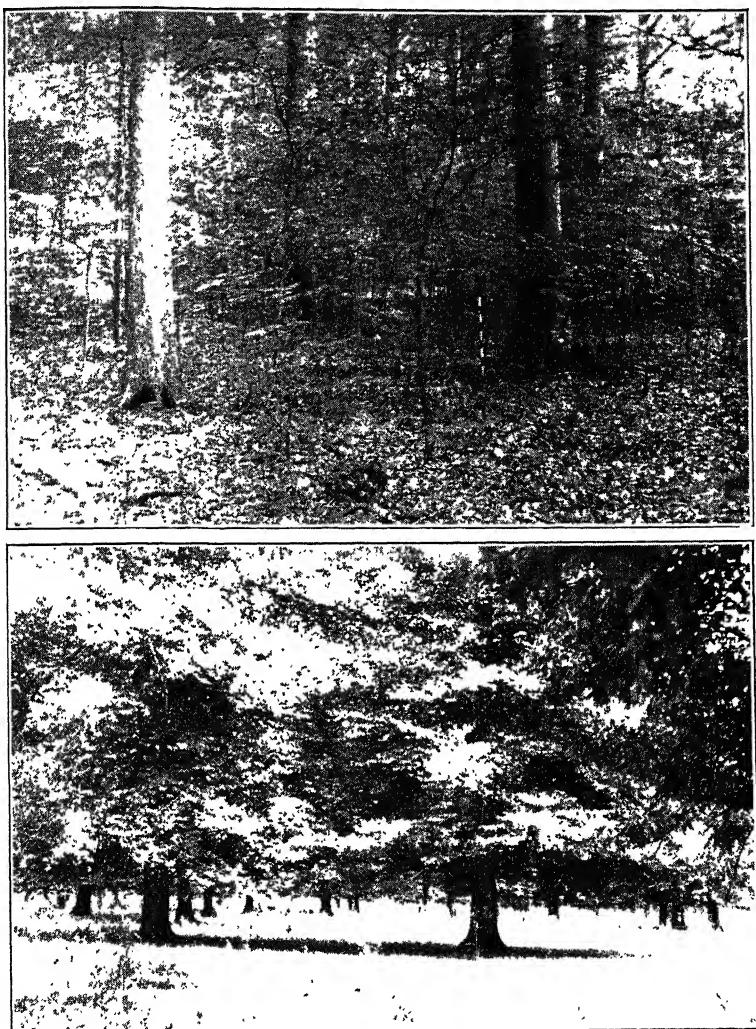


Fig. 73. (Upper) Virgin sugar maple-beech forest in central Indiana, showing an abundance of reproduction and a forest floor carpeted with leaf litter. (Lower) Similar forest type in the same region that has been subjected to heavy grazing and browsing by cattle. Forest reproduction has been eliminated, so that there will be no young trees to replace the old ones when they die. The ground is covered by a *Poa pratensis* sod which provides good pasturage. A scattering of the unpalatable *Veronica altissima* indicates that the sod has been weakened by overgrazing.

ground, but with rare exceptions this method has proved unsuccessful chiefly on account of the biotic factor.⁵⁰⁷ A degree of success can be achieved when the seed is broadcast on areas within a few months after they have been denuded by fire. The barren condition created by the burning drives most rodents and birds out of the area, and seedlings may have a chance to become established before vegetative cover attractive to these animals is reestablished. Under certain circumstances the extensive use of rodent poisons may be warranted in good seed years to insure the survival of adequate crops of seedlings.

Not only are seeds consumed by animals, but during their first summer seedlings remain so succulent that they are subject to attack by rodents, wireworms, etc. Also, grazing animals may cause much damage to seedlings by trampling and browsing them.⁵⁰⁸ Where snow cover limits the availability of winter forage, and the populations of game animals or livestock are heavy, all woody plants within reach may be browsed until killed. This is most detrimental to young trees and shrubs that protrude but slightly above the snow, and it is obvious that continued browsing of these plants eventually destroys woody vegetation for lack of replacement of old trees and shrubs as they die (Fig. 73).

Aquatic Plants as Animal Food

The economic importance of ducks, muskrats, fish, and other aquatic animals has stimulated considerable interest in the hydrophytes that provide them with food and shelter. Techniques for making inventories, for planting desirable species, and for destroying worthless kinds have been developed.⁴²²

Management of the margins of bodies of water impounded for irrigation presents an especially difficult problem. Because depth of water is so important a factor in the autecology of rooted plants, most of them cannot grow where there is an appreciable annual "draw-down" of water. Instead of supporting a dense growth of food and cover plants as would ponds of equal size, the margins of such reservoirs are characterized by barren aprons which are somewhat of an erosional problem and consequently contribute to turbidity and sedimentation (Fig. 74). Birds and mammals are largely excluded by these conditions, though fish do not fare so badly because



Fig. 74. Eroded apron about a mountain lake dammed up as an irrigation reservoir. Southern Idaho.

their food chains are based upon plankton organisms that are not disastrously affected by the annual draw-down.

Exclosure Technique

A simple but effective method of studying the effects of herbivorous animals on plants is by *exclosures*. A fence or other type of barrier is constructed to exclude a particular class of animals from a small experimental plot which can thereafter be compared with adjacent but unprotected areas. The size and method of construction of an exclosure depends on the type of animal to be excluded. Small conical tents of hardware cloth are effective to protect seedlings and other small experimental plants against mice or other rodents and birds. Shallow boxlike cages of chicken wire have been used to exclude birds. Suitable types of fencing material have been widely employed in studying the influences of large rodents, sheep, cattle, deer, etc.

Exclosures that are maintained for a considerable length of time

permit an evaluation of the net effect of animals on the surrounding vegetation and provide a basis for making beneficial adjustments in range use.¹³⁶ These areas also show which changes in vegetation are the result of climatic cycles and weather rather than of grazing pressure. When an exclosure is established after an area has been badly overgrazed recovery may be slow in spite of release from grazing pressure because the current phase of a climatic cycle may be unfavorable to seedling establishment or because certain species have been so completely eliminated that no adequate seed source remains.

Temporary exclosures which are moved from place to place permit the measurement of plant production during each season as well as an evaluation of the quantity of forage consumed by animals. On such plots forage is commonly measured by clipping and weighing the oven-dry material. When movable exclosures are used, it is important to select different parts of the grazed area for experimental and control plots each year in order to rule out effects carried over from preceding years. Some attempts have been made to simulate grazing by clipping, but the natural forage preferences of animals, together with their trampling and manuring effects, greatly reduce the significance of such studies.^{236, 326} However, clipping grasses and the new growth of shrubs allows a study of the extent to which the plants can endure regular loss of photosynthetic organs and still remain in a fair state of vigor.

It should be obvious that the fence or screen used in constructing an exclosure will promote the drifting of snow and deposition of dust, will provide some shade, and will interfere with normal air movement.¹⁵⁰ Since the object of exclosure studies is the control of but a single factor of plant environment, namely herbivore pressure, the utmost attention should be directed to the problem of minimizing the effects of the barrier on physical factors. This is accomplished by using exclosures of the largest size and of the lowest and most open structure that will possibly give the desired type of protection. The degree of success in this respect can be estimated by comparing evaporation rates and other factor intensities within and without exclosures.

Enough toxic zinc can wash off rustproof metal netting to account for most of the vegetation changes induced by a small cage used as an exclosure.²⁶⁴

Large exclosures tend to divert the movements of excluded livestock, so that areas selected outside for comparison must be situated

where they will be free of paths used in passing around the enclosure.

A final difficulty that must be guarded against is that the establishment of an exclosure, especially of the small fenced type, may encourage the development of an abnormal rodent population on the area.

CARNIVOROUS PLANTS⁴⁰³

Pitcher plants are any of a number of species belonging to the genera *Sarracenia*, *Darlingtonia*, *Nepenthes*, etc., the leaves of which are somewhat pitcher-shaped and partly filled with liquid (Fig. 75).



Fig. 75. Pitcher plants. (Left) *Sarracenia flava* growing in Georgia. The opening to the pitcher is directed upward and is sheltered by a bright-yellow, umbrellalike flap supported at one side by a maroon-colored stalk. (Right) *Darlingtonia californica* growing in Oregon. The opening is on the bottom surface of the curved, bright-yellow upper part of the leaf.

This liquid is partly or entirely an excretion from the leaf surface and, in some species at least, has been shown to be essentially an aqueous solution of proteolytic enzymes.¹⁶⁹ Insects and other small animals wandering into the leaf commonly drown in the liquid because their efforts to escape are thwarted by downward-pointing hairs or an extremely smooth vertical surface. Enzymes dissolve the softer parts of the bodies, thus providing soluble amino acids that can be absorbed by the leaf. Wholly unrelated to this nutritional phenomenon is another relationship that pitcher plants commonly maintain with other kinds of animals. Certain protozoa as well as the larvae of a few dipterous insects are able to resist the enzymatic action and live within the pitcher fluid.⁵²³

Sundews (*Drosera* spp.) comprise a genus of small herbs which are widely distributed in boggy habitats. The leaf blades are somewhat orbicular or spatulate, reddish, and covered with prominent gland-tipped hairs, each of which bears a glistening droplet of a sticky fluid. Small insects alighting on the leaves become stuck to a few of these hairs, and this stimulus causes other hairs to bend over so that most of the glands touch the body. The same stimulus causes the glands to secrete proteolytic enzymes that digest certain parts of the insect body, then when the digestible parts are absorbed the hairs resume their former position and are ready for another victim. It is interesting to note that materials containing no protein fail to stimulate the movement of the hairs or the secretion of enzymes!

The aquatic bladderworts (*Utricularia* spp.) are delicate herbs that bear bladderlike traps 5 mm or less in diameter. These traps have trigger hairs attached to a valvelike door which normally keeps the trap tightly closed. The sides of the trap are compressed under tension, but when a small form of animal life touches one of the trigger hairs the valve opens, the bladder suddenly expands, and the animal is sucked into the trap. The door closes at once, and in about 20 minutes the trap is set ready for another victim. A single plant bearing a number of traps that work at this speed can capture a great many small animals each day.

The leaf blade of the Venus flytrap (*Dionaea muscipula*) superficially resembles a steel trap, and the red upper surface bears six sensitive hairs which, if contacted, cause the leaf to close suddenly. Subsequently digestion and absorption take place; then the leaf blade resumes its original open position.

None of the above carnivorous vascular plants seems in the least dependent upon its animal prey for nitrogenous compounds; there-

fore it must be concluded that the carnivorous habit is only an incidental feature of their nutrition. However, many fungi that parasitize man and other animals are obligate carnivores. Certain aquatic fungi (e.g., *Dactyella bembicoides*) possess looped hyphae that constrict and hold any wormlike animal that crawls through the mycelium; in others (e.g., *Zoophagus insidians*) hyphae serve as bait and suddenly expand when engulfed by a feeding animalcule, thus effecting its capture. *Arthrobotrys entomophaga* captures insects by means of adhesive secretions from the ends of specialized hyphae.¹⁷¹

POLLINATION BY ANIMALS

The cross-pollination* of most showy or odorous flowers is secured by flying insects, chiefly bees, butterflies, moths, and flies. These insects are by far the most important group of animal pollinators, but other kinds of animals occasionally perform this function. Hummingbirds and the sunbirds are the ecologic equivalents of insects in this regard. Bats,¹⁷⁴ rats, and snails also appear to be the pollinators of certain flowering plants.

Many species of plants, including such important crops as fruits, legumes, buckwheat, cucurbits, and crucifers, absolutely depend upon insects for pollination. Fruit growers and greenhouse men commonly rent hives of honeybees during the proper seasons to insure pollination. In fact, the monetary value of all the honey produced commercially is far exceeded by the value of the honeybee in pollination. Honeybees are especially efficient on account of their habit of visiting only one kind of flower on each collecting trip, thus carrying nearly pure burdens of one pollen from one flower directly to another of the same species.

Insects visit flowers either for nectar or for pollen, both of which are a source of food. It is believed that long ago some insects developed the habit of feeding on the abundant pollen of primitive flowering plants, which in the beginning were presumably anemophilous. Certain of those species of plants developed protective measures against insect marauders, such as unpalatable pollen or a very

* The broad evolutionary significance of cross-pollination will be brought out by the discussions in Chapter Ten. However, at this point it may be stated that self-pollination in wild plants is not particularly detrimental, although cross-pollination is of distinct advantage in permitting a maximum degree of adjustment to existing environmental conditions.

short period of pollination, and thus became obligate anemophiles. Others found the insect visitations beneficial in that the accidental distribution of pollen by the insect as it flew directly from flower to flower proved far more economical than the wind method. These plants became *entomophilous* by developing adaptations favoring insect pollination: showiness due to the color, size, or aggregation of the flowers into clusters; fragrance due to volatile oils; perfect flowers with stamens and pistils that are scarcely if at all exerted, but instead are strategically located with respect to the insect's path. Their pollen is always sticky and often rough or spiny so that it adheres to an insect's body but is not readily picked up by wind. This pollen is not produced abundantly unless, as in poppy, it remains as the principal inducement to visitation. Although there are many flowers that are regularly cross-pollinated by insects without possessing devices more specialized than the ordinary features just enumerated, others exhibit an infinite variety of highly specialized features that tend to insure this service. Some of these special adaptations are as follows.³⁵⁶

Berberis and *Kalmia* have stamens that are reflexed until an insect scrambling over the flower causes them to spring inward and dust pollen on its body. In alfalfa and other legumes the stamens and stigma are held in the keel under tension and are freed ("tripped"), striking the under part of the body, when a bee depresses the keel to get at the nectar. When pollen dusting is as indiscriminate as in these flowers, partial or complete self-sterility or the maturation of stamens and pistils at different times (*dichogamy*) is necessary if self-pollination is to be prevented.

Catalpa, *Tecoma*, and *Utricularia* have lobed stigmata with the stigmatic surfaces on the inner faces. A few seconds after an insect contacts these stigmata they close together, thereby guarding against self-pollination and possibly aiding the germination of the first pollen received.⁴⁸²

The perianths of *Aquilegia*, *Delphinium*, and *Viola* have deep spurs into which nectar is secreted. These are always located so that insects normally must crawl into the flower and brush against the stigmata, then the anthers, to get the liquid. Though the nectar contained in the long spurs is normally available only to those insects possessing long proboscises, certain others, including insects and hummingbirds, have learned to steal the nectar without entering the flower by puncturing the lower end of the spur from without!

In *Cypripedium* insect visitors enter the inflated lip through the opening in the top but leave by means of openings in the back of the corolla; in pursuing this route they contact first the stigma and then the anther.

In *Salvia* a remarkable lever device, against which the insect's head strikes, brings the anther down on the insect's back as it enters the corolla tube.

The stamens and pistils of *Mitchella*, *Decodon*, *Pontederia*, *Primula*, and *Linum* are of two or more different lengths, a condition referred to as *heterostyly*. Pollination is effected chiefly between those organs of the same length, because that part of the insect's body that receives pollen from a long stamen comes into contact only with the long type of pistil, which occurs only on short-stamen flowers, and vice versa.

The relations between insects and flowers described thus far are the result of the insects' visitations for food, but the attractiveness of flowers to insects may result from other types of relationships. In the genus *Yucca* the sole pollinator, the female *Tegeticula* moth, carries a ball of pollen from one flower to another, thrusts this down the tubular stigma, then uses her ovipositor to place eggs among the ovules whose fertility she has just insured. A few seeds always escape destruction by the larvae, so that in the long view the *Yucca* is benefited by this relationship. Carrion insects, likewise searching for a suitable medium upon which to lay their eggs, are attracted to the ill-smelling carrion flowers such as *Smilax herbacea*, *Symplocarpus*, *Lysichitum*, and *Stapelia*. Here the insect is tricked into performing its valuable function, for in its fruitless wandering over the flower or inflorescence it accidentally transfers the pollen. Nor does the insect benefit in the following circumstance. The lip of certain orchids (*Ophrys* spp., *Cryptostylis* spp.) is constructed, colored, and scented so that it resembles the female of certain hymenopterous insects, thereby inducing males to alight and attempt copulation, which act, when repeated on different flowers, brings about cross-pollination.^{371, 761}

Specialization connected with insect pollination has tended toward parallel and complementary evolution between insects and flowers, leading to the complete dependence of one kind of plant on one kind of insect. When such an interdependence involves an economically important plant, the insect deserves special consideration. For example, numerous attempts to grow marketable quality Smyrna figs in California were unsuccessful until finally the pollinating wasp

Blastophaga grossorum became established. Again, the production of red clover seed in Australia became possible only after the bumblebee was introduced, for the flowers are usually too deep for honeybees to reach the nectar. *Vanilla* must be pollinated by hand if grown out of the range of its special pollinating insect.

Extreme specialization is as dangerous in connection with pollination as with other functions in the biologic world, for not only must the ranges of the two symbionts coincide but also the extinction of one heralds the doom of the other. *Yucca* and *Tegeticula* appear to have reached the final stage where each is dependent on the other, but such a degree of interdependence is not common, perhaps for the simple reason that the situation is too precarious to endure for long.

The interrelations between flowers and insects is a fascinating topic on which there is much literature but little consistency in experimental results.¹²⁵

DISSEMINATION BY ANIMALS (ZOOCHORY)

Edible Disseminules

Disseminules ingested but not digested (endozoochors). The seeds of berries and other small fleshy fruits are encased in succulent tissues which are used by birds as food, yet in many of these fruits the seeds (*Ribes*, *Rubus*), achenes (*Fragaria*), or stones (*Elaeagnus*, *Prunus*) have thick coverings and so pass through the digestive tracts uninjured to be carried some distance before being excreted.¹²³ This is, of course, the fate of only those hard seeds or stones that are swallowed whole, for such birds as grosbeaks that crack the hard coverings to extract the soft endosperm and embryo destroy rather than disseminate seeds. The passage of seeds through a digestive tract facilitates germination in certain species.

Cattle readily eat the sweet pods of *Prosopis*, but many of the hard seeds escape injury during mastication and pass unharmed through the digestive tract. Cattle are known to disseminate *Berberis vulgaris*³⁴⁰ and herbaceous weeds,⁵⁶⁷ and jack rabbits disseminate *Opuntia*.⁶⁷³

The spores of stinkhorns pass uninjured through the digestive tracts of the carrion insects that feed on the hymenium of these fungi.

Disseminules with only accessory tissues ingested. The seeds of the mistletoe *Phoradendron* may be lodged on new hosts by the act

of a bird wiping its bill after feeding on the sticky berries. Even ants have been observed transporting seeds that are oily or have fleshy appendages.

Disseminules cached but not recovered. Rodents and birds are suspected of hiding many seeds which they subsequently fail to recover, and which may be situated in a position favorable for germination. Apparently this is the only manner by which plants with heavy disseminules such as *Juglans*, *Carya*, and *Quercus* can extend their distribution upslope.²⁴³ The value of rodents in this respect is easily overestimated, for their ability to detect the presence of buried seeds under experimental conditions is remarkable; probably very few seeds are not recovered except in years of exceptionally abundant supplies.

Inedible Disseminules (Epizoochores) ✓

Specialized for clinging. Burlike fruits or inflorescences, such as those of *Arctium*, *Bidens*, *Cenchrus*, *Desmodium*, and *Xanthium*, are especially well adapted for clinging to the fur of animals which carry them some distance before chewing them from their fur or shedding them with it. Ecologically related but certainly less pleasant types of disseminules are found in species of *Opuntia* and in *Stipa*, in which backwardly barbed spines cause the stem segments and florets, respectively, to become anchored in the flesh of animals that come in contact with them. Adhesiveness in *Adenocaulon bicolor* is accomplished by glandular hairs covered with a gummy excretion. In fungi belonging to *Phallales* and mosses in the genus *Splachnum*, the spores are transported by insects which are attracted to the plants by foul odors.

Unspecialized. Mud clinging to the feet of migratory water birds has been found to contain a wealth of tiny disseminules of aquatic plants—a fact that explains the appearance of such plants within a very short time after any suitable body of water accumulates. Spores of many kinds, including those of fungi causing important tree diseases, have been isolated from the plumage of migratory arboreal birds.²⁷⁶ Many plant pathogens are carried from host to host by insects. Such important diseases as the Dutch elm disease, cucumber wilt, and typhoid fever are transmitted by these organisms.

Man's activities have allowed many plants to extend their ranges in the last few centuries. The facts that rare weeds first make their appearance along railroads and that many plants are common only

on ballast dumps indicate important means of dissemination. Weed seed unintentionally included with grain, and diseases in imported nursery stock, constitute other important methods by which plants are spread. Examples of the effectiveness of these two methods are provided by the history of Russian thistle (*Salsola pestifer*) and of white pine blister rust (*Cronartium ribicola*) in North America.

LIANAS

Vascular plants that are rooted in the ground and maintain their stems in a more or less erect position by making use of other objects for support are called vines or *lianás*. This habit of growth has the advantage of enabling the plant to get better light with a maximum economy of supporting tissues. Those lianas that climb over other plants are, in a sense, parasitizing the other plants' supporting tissues, but there is no direct nutritional relationship between true lianas and the trees upon which they grow. Lianas, however, do show all degrees of intergradation with climbing parasites.²⁸⁷

Anatomically liana stems usually exhibit two peculiarities: the woody cylinder occurs as strands separated by vertical partitions of parenchymatous tissues, and the xylem vessels are long and wide. The first of these characters may be looked upon as an adaptation favoring suppleness, which may be of advantage in accommodating flexion resulting from unrigid supports. The superior conductance of the wood may be necessary because the stem remains relatively slender yet supports considerable foliage at its summit.

The abundance of lianas varies directly with the humidity and warmth of the climate, so that this ecologic class is most conspicuous in the moist tropics. They are of minor economic importance in forestry in three ways. In the tropics the trees may be so thoroughly woven together by myriads of woody vines that an individual will not fall when cut, thus necessitating the felling of trees in groups. Also, by the constriction which develops as both tree and vine grow, a woody twining liana inhibits downward translocation with the result that the rate of increment in the supporting tree is increased above and decreased below the point of stricture (Fig. 76). Although the tree may be killed in some instances, in others new conductive tissues may form that have a spiral orientation in harmony with the spiral course of the liana stem, or possibly natural root grafting may prevent starvation until the constricting stem is engulfed.⁴¹⁸ Woody

Fig. 76. Sectioned stem of *Amelanchier florida* showing the effects of constriction by the woody liana *Lonicera ciliosa*. Interference with downward translocation of foods in the tree has allowed a greater amount of wood to form on the upper side of the constriction.



vines frequently spread their canopies over those of the trees they climb and thus interfere with their normal growth.¹⁹³

Lianas may be conveniently classified according to the following scheme which emphasizes increasing degrees of specialization:

1. *Leaners*. Those plants that have no special devices for holding onto a support, e.g., *Plumbago capensis*.

2. *Thorn lianas*. Lianas possessing thorns or prickles which are hardly specialized for the function of climbing but which prove of definite passive value in this regard, e.g., rambler roses, *Bougainvillea*, *Euphorbia splendens*, *Galium*.

3. *Twiners*. Lianas in which the entire stem twines about the support. These are mostly herbaceous plants such as *Phaseolus* and *Ipomoea*, perhaps because woody plants are at a distinct disadvantage when twined about trees with secondary growth. As mentioned above, woody twiners such as *Celastrus scandens* and *Lonicera ciliosa* become deeply imbedded in the tissues of the supporting trees so that the continued growth of both tree and vine is impaired (Fig. 76). With but few exceptions the direction of twining in this class of lianas

is either constantly clockwise or constantly counterclockwise among the individuals of a taxon.

4. *Tendril lianas*. Lianas possessing special organs, the tendrils, which are modified to facilitate climbing either by twining about the support (*Vitis*) or by adhering to its surface (*Hedera helix*). Tendrils are generally weak organs until they become attached, but subsequently their mechanical tissues develop to such a striking degree that an individual tendril becomes capable of supporting great weight. Before they have made contact with a support they are very sensitive and may respond to a stimulus of touch lasting only a few seconds. Tendrils may be parts of leaves, such as the modified terminal leaflet of a compound leaf (*Pisum*, *Vicia*), or the modified tip of an acuminate blade (*Gloriosa*), or the petiole which takes a turn about the support (*Clematis*). In *Vitis* the tendril is of stem origin. Adventitious roots emerge from the stems of *Vanilla* and *Parthenocissus* to serve as tendrils.

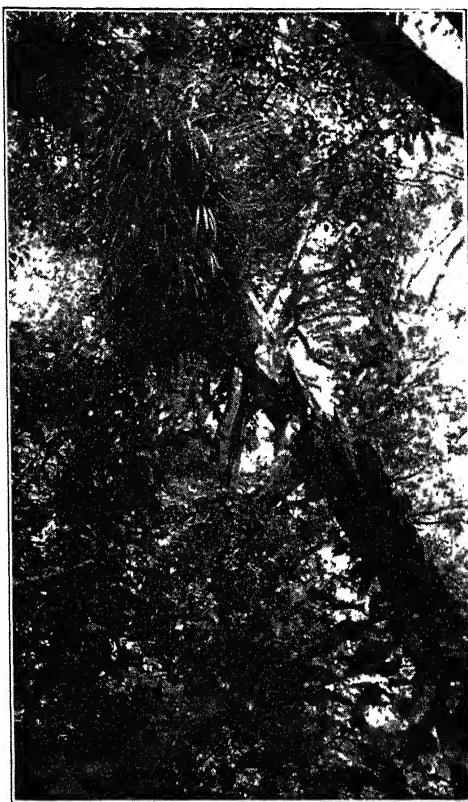
EPIPHYTES ^{144, 489}

Epiphytes are plants growing perched on other plants, which differ from parasites in not deriving water or food from the supporting plant and from lianas in not having soil connections. Of all ecologic classes of plants these are the most directly dependent on precipitation for their water supply, and unless rains or heavy dew fall at frequent intervals they must be able to endure drouth. Their nutrient supply is derived in part from rainwater, which always contains some dissolved substances,^{281, 314} in part from accumulated wind-borne particles, and in part from the decaying bark surface of supporting plants.

Epiphytes may grow on trees, shrubs, or larger submersed plants. They occur on the trunk, limbs, and sometimes on the upper leaf surfaces of woody plants. When in the last position they are called *epiphylls*.^{152, 520} They are especially abundant in the forks of trees and on horizontal limbs, on which habitats a considerable depth of soil can collect (Fig. 77). They are least abundant on vertical and smooth surfaces.

As indicated above, the greatest single vicissitude of the epiphytic habitat is drouth, and these plants are most abundant where drouth is never protracted. In cold or dry climates epiphytes are few and consist chiefly of algae, lichens, liverworts, and mosses. In warm wet climates these groups are augmented by a wide variety of vascular plants, especially ferns and species belonging to the bromelia and

Fig. 77. Luxuriant rain-forest vegetation with an abundance of epiphytes and lianas. Tamazunchale, Mexico.



orchid families. The rich epiphytic flora of a tropical rainforest shows a remarkable gradation from sciophytic hygrophytes, confined to the lower trunks of the trees, to xerophytes (including cacti!) that demand bright light but can endure the occasional desiccation of the treetop habitat. Frequently epiphytes show marked preferences for particular supporting species.⁴¹ The moss *Tortula pagorum* is abundant in southeastern North America only on the bark of trees located in cities, apparently requiring some air-borne constituent of smoke.¹⁴ Some epiphytes grow on rocks or insulated wires as well as on plants (Fig. 78).

There are all gradations between epiphytes and parasites,⁵²⁴ and also between epiphytes and lianas. Some, as the fern *Nephrolepis*, are at first rooted in the soil, then by extending their rhizomes up a tree trunk and later losing connection with the ground they eventually

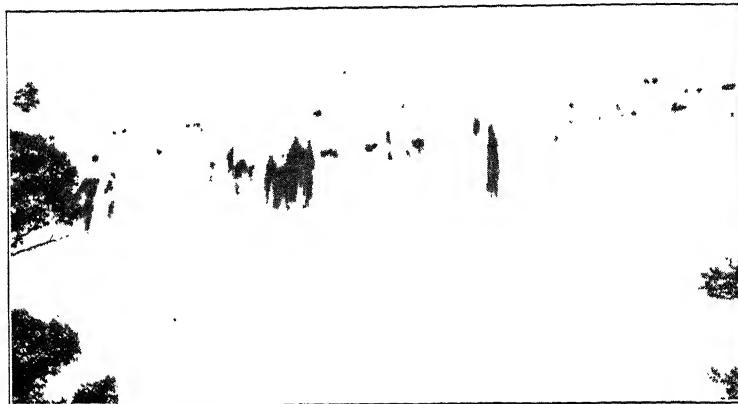


Fig. 78. *Tillandsia usneoides* (the pendant Spanish moss) and *T. recurvata* growing on insulated wires in Sebring, Florida.



Fig. 79. A young tree of *Tsuga heterophylla* that germinated approximately 5 meters (see meter stake) above the ground on the trunk of an older tree of *Pseudotsuga menziesii*. This phenomenon is limited to regions such as the Olympic Peninsula, Washington, where the bark surface is continuously moist.

become epiphytes. Other plants, such as the hemlock *Tsuga heterophylla* (Fig. 79) and the strangling figs (Fig. 80), germinate on trees but live as epiphytes only until their roots grow down over the surfaces of the trunks and establish connections with the soil.

True epiphytes have soil connections at no time during their life cycles, and they frequently show marked adaptations favoring their mode of living. Xeromorphy, such as thickened cuticles, sunken stomata, and succulence, is common. Some epiphytes spread their roots over the plant surface in such a manner as to be well situated to absorb water from the film deposited by even a small shower. In others, the *nest epiphytes*, the roots accumulate large masses of debris that hold water like a soil. The roots of many tropical epiphytes in



Fig. 80. (Left) Strangling fig becoming established as an epiphyte in the crown of a palm. (Right) An old strangling fig, the roots of which have fused to form a hollow "trunk" about the lower part of the palm. The fig is beginning to shade out the palm and will eventually bring about its death. Mexico.

the orchid and arum families extend outward into the air, appearing as thick, unbranched, whitish organs. Covering the surface of these roots is a special layer of empty, whitish cells that can take up water rapidly from even a brief shower; afterward the living core of the root absorbs the water from this storage layer. The special absorptive tissue is called *velamen*.

Among the epiphytic species of *Tillandsia* (Bromeliaceae) the roots serve chiefly as anchorage organs, the leaves and stems taking over the function of absorption. In *T. usneoides*, "Spanish moss," the finely divided shoot system is covered with peltate scales that collect capillary water and allow it to be absorbed by the small uncutinized spots on the epidermis which they shelter during times of drouth (Fig. 78). The leaves of other species of *Tillandsia* may be shaped like gutters (Fig. 81) and so collect water in their axils. These are *tank* or *cistern* epiphytes. Numerous aquatic vertebrates, including mosquito larvae, live in these tiny cisterns, so that they have been described as a vast interrupted marsh extending across the tropical forest, rendering the problem of mosquito control difficult. Among the most specialized of epiphytes is *Dischidia*, the leaves of which form pitchers that accumulate water and leaf litter, and into which special absorptive roots extend!



Fig. 81. A tank epiphyte (*Tillandsia* sp.) growing on the trunk of a palm. Sebring, Florida.

PARASITIC VASCULAR PLANTS¹³⁷

Dodder (*Cuscuta* spp.) is a widespread, threadlike twining herb growing on other vascular plants. Its seeds germinate to produce slender green stems that grow over the soil surface until they reach a suitable host about which they twine. Adventitious roots emerge from the dodder stem to penetrate the stem of the host, where they make contact with both xylem and phloem. These specialized roots, as well as other kinds of absorptive organs of parasites, are called *haustoria*. Once established on its host the dodder loses connection with the ground but continues to grow by extracting water and foods from the host plant, and eventually it produces flowers and seeds. Dodder is leafless and has a yellowish-brown color, but the stems contain chlorophyll so that the plant is completely dependent upon its support only for water.⁶⁹⁶ It is therefore most properly called a *partial parasite*. Dodder becomes a troublesome weed at times, especially in fields of flax or red clover.

The genus *Cuscuta* is usually placed in the Convolvulaceae, so that it appears that dodder represents a further step in specialization beyond that of the green but lianoid bindweeds and morning-glories. Closely similar to dodder in form and nutrition is *Cassytha*, which, however, belongs to the Lauraceae.²⁶⁸

Broomrapes (*Orobanche*, *Conopholis*, *Epifagus*, and others of the Orobanchaceae) are herbs completely parasitic upon the roots of seed plants. The roots of their seedlings are connected to the roots of suitable host plants, and in some cases the seeds will not germinate unless they are in contact with the root of a suitable host. The aerial parts are no more than brownish inflorescences lacking chlorophyll. This family is closely related to the Scrophulariaceae, in which many common genera are facultative root parasites.*

Rafflesia (Aristolochiaceae) is a genus of Malaysian plants parasitic upon the roots of *Vitis*. This parasite has become so extremely degenerate that it resembles a fungus, for the vegetative parts are mycelioid and wholly contained in the roots of its host. One species, *R. arnoldi*, is famous for bearing ill-smelling flowers about a meter in diameter, these being the only organs to appear above the ground.

Mistletoes (Loranthaceae) are dwarf, shrublike plants growing

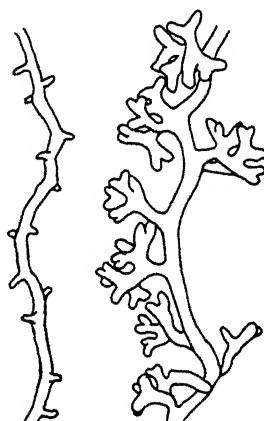
* The family Santalaceae also furnishes many apparently autotrophic plants that are root parasites.^{173, 545}

There is great variation in the anatomy of mycorrhizae on different plants and in the nature of the interrelationship between the two organisms. Apparently every gradation exists from outright parasitism to conditions of controlled parasitism in which the higher plant turns the fungal invasion to good advantage. The three groups of plants that have been studied most intensively from this standpoint are the Pinaceae, Orchidaceae, and Ericaceae, and these will be discussed briefly.

Pine Mycorrhizae⁴⁴

Pine rootlets, as well as those of many other trees, are divided morphologically into the long roots (the main axes) and the short roots, the simple laterals emerging from the former. In fertile soils the rootlets are not mycorrhizal, the root-hair zones of the dominant long roots absorbing almost all the water and nutrients used by the tree.²⁷² On the other hand, in soils deficient in N, P, K, or Ca, which is a common condition, the absorptive powers of the long roots seem to be inadequate, and the short roots are invaded by fungi that take over the absorptive functions. As a result of the fungal invasion these short roots are stimulated to branch repeatedly so that they become coraloid in appearance, the degree of branching being inversely proportional to the degree of fertility (Fig. 82). These short roots thus become mycorrhizae which are definitely more efficient than an uninfected root because of the tremendous aggregate surface of the long hypae extending into the soil. Where the fungus is

Fig. 82. Rootlets of *Pinus strobus*. (Left) Nonmycorrhizal rootlet. (Right) Mycorrhizal rootlet. Hyphae and root hairs have been omitted. (After Hatch, 1937.)





CHAPTER EIGHT

The fire factor

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Except in very wet, very cold, or very dry regions, fire has always been an important factor in terrestrial environment. Charred fossils show that lightning-started fires have periodically ravaged land vegetation since its earliest appearance on earth. To this eventually was added the effect of primitive man who, for a variety of reasons, periodically set fire to vegetation. With the spread of civilization man-caused fires have become far more numerous than those caused by lightning, but the abundance of roads and plowed fields in well-

populated regions, together with efficiently organized fire prevention and control agencies operating on forest lands, prevent individual fires from spreading far as a rule.

Fire injures plants directly by subjecting the tissues to lethal temperatures, but many other ecologic aspects of fire do not involve the temperature factor.

KINDS OF FIRES

Wherever the soil is overlaid with thick accumulations of organic matter, the latter may catch fire and smolder for long periods. This may happen even though the material is moist, for the front of active oxidation moves forward so slowly that the heat from it dries out the adjacent unburned debris at an equal rate, thus perpetuating a zone of combustible fuel. Fires of this type that are flameless and subterranean are called *ground fires*. They kill almost all plants rooted in the burning material, although old woody plants may survive if their large roots have thick bark and descend well below the organic material.

Fire often sweeps over the ground surface rapidly, the flames consuming litter, living herbs, and shrubs, and scorching the bases of any trees it may encounter. These are called *surface fires*, and if there is no thick horizon of litter and duff that contains most plant roots, subterranean organs and buried seeds may escape serious injury.

In dense woody vegetation fire may travel from the canopy of one plant to another. Such fires are called *crown fires*. Usually everything from the ground upward is consumed, or at least killed (Fig. 84), but sometimes the ground is moist enough so that many subterranean organs and buried seeds escape destruction.

When burning conditions change, one of the above types of fire is frequently converted into another. Ground fires especially are likely to smolder for many days before a wind whips up the glowing material into active flame and a surface or crown fire results.

ADAPTATIONS RELATED TO FIRE

In regions where there is a heavy vegetation cover coupled with one or more dry seasons, environmental selection may have included the fire factor for so long that plants have developed special adaptational features that favor persistence under repeated burning.



Fig. 84. Photograph taken of a forest interior only a few days after a devastating crown fire had swept the area. All large trees were charred and killed; small trees, shrubs, and herbs were entirely consumed. The mineral surface is covered by about 2 cm of fluffy ash.

Whether the herbaceous perennial life form of grasslands has developed in response to the fire hazard or not, it has proven invaluable in a vegetation type that is very susceptible to burning.

Germination

Certain taxa of shrubs in *Arctostaphylos*, *Ceanothus*, and *Rhus* produce large quantities of hard-coated seed that tend to lie dormant in the soil until the scrub in which they occur is burned. Fire cracks the seed coats and then seedlings appear in large numbers.⁶⁵⁴. In the laboratory treatment with water at 80° C or dry heat at 110–115° for 5 minutes is useful in obtaining maximum germination of these plants.⁷⁴²

Rapid Growth and Development

Certain woody plants that are killed by fire but have fire-resistant seeds or fruits have developed an ability to fruit only a few years

after germination, so that the life cycle is completed before enough debris accumulates for another devastating fire.²²⁴ *Pinus muricata*, for example, may start to produce cones when it is only a meter tall.

A unique degree of immunity from the effects of surface fires is possessed by the seedlings of *Pinus palustris*, the longleaf pine of southeastern North America. The terminal bud remains close to the ground for about five years after germination, and during this time it is located in the center of a radiating hemisphere of long needles that do not burn readily. Although fire results in high mortality the first and second years, subsequently light fires do no more than scorch the tips of the needles. After the seedling has developed an efficient root system, the shoot begins to grow rapidly, carrying the all-important apical bud above the zone of potential injury. This stage of development constitutes a second critical period, for the slender stem is now exposed to fire, but in about three years the bark becomes thick enough to enable the young tree to survive fire again.

Fire-Resistant Foliage

Although the high resin or oil content of most conifer needles, *Ulex europaeus* leaves, and *Betula* bark allows the living tissues of these plants to burn readily, other woody plants may have so little of these compounds that the water content of the leaves may stop a surface fire where a dense canopy extends down to the ground.¹⁹

Fire-Resistant Bark

Quercus borealis, *Thuja* spp., *Pinus strobus*, and *P. contorta* var. *latifolia* have thin bark and are usually killed when surface fires sweep the area in which they are growing. In contrast, *Quercus macrocarpa*, *Larix occidentalis* (Fig. 85), *Pinus palustris*, and *P. ponderosa* have thick bark and often escape injury when associated species are heavily damaged or killed. Elevated canopies and evanescent lower branches tend to make the insulating value of thick bark more effective.

Adventitious or Latent Axillary Buds

Pinus rigida and certain taxa of *Eucalyptus*²¹⁹ have a remarkable ability to regenerate branches along the trunk from adventitious or latent axillary buds, even after a crown fire has swept through the

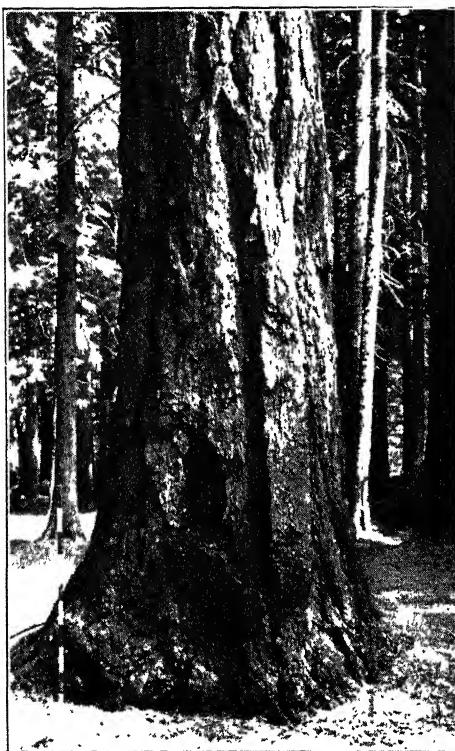


Fig. 85. *Larix occidentalis*, a tree with remarkably thick and fire-resistant bark that can endure rather hot fires.

trees (Fig. 86). Many other woody plants, e.g., *Betula papyrifera*, *Sequoia sempervirens* (Fig. 87), *Chrysothamnus* spp., and *Vaccinium* spp., produce new shoots after fire destroys the old ones, these arising from adventitious buds at the base of the root. In *Populus tremuloides* killing the shoot stimulates the growth of sucker shoots from adventitious buds arising on shallowly placed lateral roots at some distance from the old trunk.

Lignotubers

In the chaparral vegetation of Europe, North America, and Australia many shrubs (in *Arctostaphylos*, *Eucalyptus*, etc.) have evolved *lignotubers* which facilitate shoot replacement after a crown fire.^{31,32} A lignotuber is a conspicuous turnip-shaped or tabular swelling (up to 4 m across!^{32,33}) of the axis, mostly or entirely below the ground

surface, which bears latent buds and has the capacity to produce new shoots quickly because it contains food reserves. It represents a further degree of specialization beyond plants that can sprout from an unmodified root base.

Serotinous Cones

In a number of Coniferae ripe cones remain on the trees, retaining viable seeds for many years, and the term *serotinous* (meaning late to open) is used for the cones as well as the taxa. In *Pinus contorta*



Fig. 86. Sprouts arising from the trunk of *Pinus rigida* a few months after a fire. New Jersey.

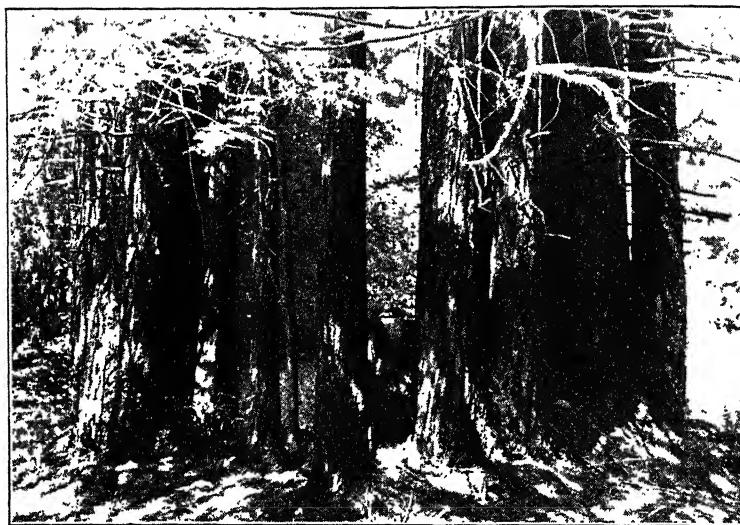


Fig. 87. Circle of redwood (*Sequoia sempervirens*) sprouts around the burned-out stump of the parent tree. California.

var. *latifolia* most cones open within a decade, but some retain viable seed for 75 years.¹²² Normally secondary growth eventually causes the pedicel to break, and with the vascular water supply cut off the carpels dry and open, allowing the seeds to be disseminated. Vegetation fires cause these cones to open promptly because the death of the tree stops the ascent of water. Fire may also favor opening by burning surface coatings of resin off the cones.¹ In addition to *Pinus contorta* mentioned above, some other representative North American conifers with serotinous cones are *P. banksiana*, *P. clausa*, *P. leiophylla*, *Cupressus sargentii*, and *Picea mariana*.³⁸⁸

INDIRECT EFFECTS OF FIRE ON PLANTS

The immediate effect of fires in killing woody plants and reducing litter to ash are readily apparent.¹ The indirect effects which ultimately result from burning vegetation are not so evident, and only recently have they been given the attention they deserve.

Removal of Competition for Surviving Species

Those species that are not killed by a fire are obviously benefited by the subsequent reduction in competition and possibly by other changes in environment that are brought about. Thus fire-tolerant species always increase in abundance at the expense of their fire-sensitive associates. In mixed stands of conifers in the northern Rocky Mountains the proportion of *Larix occidentalis* in the stand increases greatly each time the forest is swept by surface fires, for, among the old trees that survive and furnish seed for the subsequent generation, this species is best represented. After two or three fires have swept an area *Larix* may be the sole dominant, provided the intervals between fires are long enough to allow some of the trees to develop a layer of bark thick enough to withstand scorching.

Fire Injury and Parasitism

Woody plants frequently survive fires that leave large scars on their stems. The upslope sides of trees often suffer heavily in this way on account of the great accumulation of litter in the angle between the bole and the ground. Fallen logs lying next to living trees have the same effect. Where organic debris is more evenly distributed scars tend to be confined to the windward sides of the trees.¹²²

The effects of a given fire may be superimposed on the effects of one or more previous fires in that unhealed scars are greatly enlarged or the trees are burned through. This is true especially where the earlier scar has become covered with highly inflammable resinous exudations.⁶¹⁰

The larger these scars are, the more time is required for their healing and consequently the greater is the opportunity for infection by parasitic fungi and insects.^{286, 337, 650} In some regions almost all decay in timber trees can be traced to previous fire injuries. Merchantable trees that are seriously scorched should be salvaged soon after a fire if it is economically feasible.

Alteration of Environmental Factors

Almost every aspect of environment is altered when vegetation is burned. Sometimes the habitat is damaged to the extent that thousands of years are required for sufficient recovery to allow the return

of the original vegetation, but under other circumstances the effects of burning are not measurably detrimental even though environment is greatly changed. Some of the chief effects of burning will be listed below, but it should be pointed out in advance that the effects produced vary with the type of vegetation, the kind of soil, the season of burning, the prevailing weather, and other factors.

One of the most evident effects of fire is the increase in light at the ground surface that results from the destruction of plant shoots. The vegetation that quickly inhabits burned areas is usually dominated by heliophytes.

The lack of shade also allows the soil to heat up and cool off to a greater extent so that the daily range in temperature is increased. The heating effect is augmented by the blackened color of the surface so that maximal and average values are higher.²¹⁴ Ordinarily the results are a decidedly earlier development of vegetation in spring, especially the first spring following the fire,^{5, 562} and an earlier desiccation of the upper soil layers.

Rainfall interception is eliminated when the plant cover is destroyed, and, if runoff losses are not increased proportionately, the soil moisture content may rise for lack of plants to use up the water. However, the burning of surface organic matter, coupled with the effects of beating raindrops and the extermination of burrowing microfauna, usually reduces porosity, thus increasing runoff and favoring rapid erosion.²¹⁴

If fires are very hot (temperatures of 1,004° C have been recorded) litter, duff, leafmold, and at least the upper part of the humus are destroyed (Fig. 84) (Table 12). This interrupts nutrient cycles and eventually impoverishes the soil. Compounds of Ca, P, and K are changed to soluble forms which, though more readily available, are subject to rapid leaching; N is volatilized and lost (Table 12). There is a good possibility that the success of *Marchantia polymorpha*, *Funaria hygrometrica*, and other pioneer invaders of severely burned areas is due to low N requirements which allow these plants a brief period of freedom from competition from other species having higher requirements. Possibly the higher pH which usually results from the release of bases (Table 12) is also beneficial to these plants.

If fires are not very hot their effect is to increase soil fertility, at least temporarily. Apparently this is true of those fires in which temperatures just above the soil surface do not exceed about 100° C.²⁹² The release of bases, which are important nutrients, also raises the

Table 12

Comparison of certain properties of a forest soil in western Washington before and immediately after a severe fire.³¹⁶

Property	Horizon	Before Fire	After Fire
Organic matter, % dry weight of soil	A ₀	88.5	9.7
	0- 3"	5.7	3.5
	3- 6	3.7	3.1
	6-12	3.4	2.8
	12-30	2.2	2.5
Total N, % dry weight of soil	A ₀	0.9	0.3
	0- 3"	0.1	0.1
	3- 6	0.1	0.1
	6-12	0.1
	12-30	0.1
C/N ratio	A ₀	57	17
	0- 3"	27	18
	3- 6	24	18
	6-12	22
	12-30	21
Field capacity, % dry weight of soil	A ₀	190	60
	0- 3"	75	50
	3- 6	43	55
	6-12	50	57
	12-30	61	79
pH	A ₀	4.9	7.6
	0- 3"	5.0	6.2
	3- 6	4.8	5.5
	6-12	5.0	4.9
	12-30	5.1	5.2
Water-soluble salts as parts per million	A ₀	1,116	1,330
	0- 3"	370	585
	3- 6	365	164
	6-12	164	222
	12-30	82	142

pH of acid soils nearer the neutral point. This change in pH tends to favor bacterial action, especially nitrification, and thus greatly improves soil conditions for plant growth. Under these circumstances the humus remaining in the soil is mineralized rapidly so that, for

Table 13

Comparison of certain soil properties in a stand of *Pinus palustris* that has been subject to frequent ground fires, with an adjacent stand that had not been burned for 15 to 20 years.²⁹² Trenton, Florida.

Property	Horizon	Rarely Burned	Frequently Burned
Loss on ignition, %	0- 2"	2.925	2.249
	6- 9	1.346	1.152
	16-18	0.990	0.815
Total N, %	0- 2"	0.040	0.032
	6- 9	0.020	0.018
	16-18	0.012	0.011
pH	0- 2"	5.97	5.29
	6- 9	5.67	5.54
	16-18	5.75	5.58
Replaceable Ca, %	0- 2"	0.047	0.024
	6- 9	0.010	0.011
	16-18	0.008	0.009

a few years at least, the supply of nutrients is abnormally high. The plants that flourish on burned areas of this type are often species with high N requirements that cannot endure the absence of nitrate characteristic of the undisturbed forest. Burning is especially beneficial when it removes thick accumulations of organic debris with such high C/N ratios that tree growth has stagnated. Decaying roots of plants killed by the fire act as a green manure to further improve soil nutrition.

Surface accumulations of organic debris in the forest are often physically detrimental to the establishment of seedlings.^{201, 407, 412} Apparently the reason is that fluctuations in moisture content are much more violent in this material than in bare mineral soil. After fire destroys the organic layers the new seedbed conditions may permit the germination and survival of species whose disseminules had regularly perished on the area previously.

Under certain conditions the loss of humus and superficial layers of organic matter may reduce the growth-water capacity of the soil to such an extent that seedling survival is seriously reduced. The destruction of peat layers by fire has a much more undesirable effect of the same sort. These deposits are especially valuable only as peatland (water conservation, flood control, wildlife, etc.), and many

centuries are required to restore the losses due to a single burn.¹⁴⁷

Although the immediate effect of fire is to remove litter, a single burn may kill more vegetation than the dead material consumed, so that the litter cover soon becomes heavier than it was originally. When the fuel supply and fire hazard are thus increased, a secondary burn following a few years after the first may have much the more devastating effect.

The influence of fire on soil below the surface organic layers is usually slight.¹⁰ Ordinarily no more than the upper part of the humus is oxidized. However, where burning results in the replacement of fire-sensitive woody plants by grasses, the ultimate effect of the fire may be to raise the humus content above the initial level within a few years. If herbaceous legumes are favored by fire, the N content of the soil is likewise increased.

Finally, of great importance is the change in animal life brought about by fire. The new conditions favor new kinds of animals having different requirements for food and cover. The significance of the temporary exodus of seed-consuming rodents from burned forest areas has already been discussed. Birds that prefer open vegetation congregate on burned areas and carry in seeds from plants growing on other burned areas that they have visited. Thus a dense scrub of *Rubus*, *Ribes*, and other berry-producing plants may develop rapidly. The herbaceous and shrubby vegetation that dominates burned forest areas before they are again claimed by trees greatly increases the forage capacity of the land so that game animals and livestock are benefited.

The above outline, though incomplete, is sufficient to show that the relations of fire to environment are very complicated and difficult to appraise.

Stimulating Effects

Wholly aside from the matter of release from competition, fire sweeping an area frequently seems to have a stimulating effect on certain survivors. These effects are attributable to one or more of the environmental changes discussed immediately above.

Epilobium angustifolium, commonly called fireweed, is a long-lived forb that is conspicuously stimulated by burning. Dwarf sterile specimens are commonly encountered in forests that have not been burned for centuries, but the plants are so small and scattered as to escape notice. When fire destroys the trees these dwarfed *Epilobium*

plants develop to many times their former size and flower abundantly. This species produces such great numbers of comose seeds that, even in the absence of an external supply of seeds, the few stimulated plants on a burned area can give rise to a dense stand of fireweed within a year or two after the forest is destroyed.⁴⁷⁴

Populus tremuloides is a small tree peculiar for the fact that seedlings rarely survive, but once one does a grove is usually formed by suckers that rise from shallow horizontal roots radiating from the initial tree. The *Populus* stands thus formed are relatively permanent, maintaining themselves by continued suckering. Fire usually kills the thin-barked shoots, but the roots are only stimulated to sucker the more vigorously. Apparently the additional solar radiation absorbed by the bare and blackened soil surface is responsible for the fact that on the first season after a light burn suckers appear in unusual numbers and attain a greater height.⁶⁰⁸

Although a number of grasses are easily killed by fire, some are not injured, and still others are stimulated to produce abnormally large quantities of seed. The latter include *Aristida stricta*, *Cynodon dactylon*, *Paspalum notatum*, and *Sporobolus curtisii*. It is significant that nitrate fertilizers have been found to have essentially the same stimulating effect as burning in *Cynodon* and *Paspalum*.⁹¹

PRACTICAL VALUE OF VEGETATION BURNING

So many variables are involved in the relations among fire, other environmental factors, and organisms that generalizations are hazardous. Sufficient careful research has been done to show that the effects of burning vary from extremely devastating to more beneficial than detrimental. Although uncontrolled burning is usually detrimental to man's interests, the usefulness of properly controlled fire in certain vegetation types can no longer be questioned.^{250, 525} Some examples of the scientifically justifiable use of fire follow.

Use of Fire to Favor Economically Important Plants

Where economically valuable species that are not destroyed by fire grow associated with relatively valueless fire-sensitive species, fire can be used to advantage in improving vegetation for the good of mankind. The aim here should be to cause the fewest and lightest

fires that will accomplish the desired vegetation changes, so that the detrimental effects of fire on the soil will be minimized.

Originally the vegetation of the sagebrush-grass semidesert of western North America consisted of a dense cover of perennial grasses among which were scattered moderate-sized shrubs, chiefly *Artemisia tridentata*. When this vegetation is subjected to heavy grazing the perennial grasses are reduced to a scattering of weakened plants, whereas the relatively unpalatable sagebrush increases in size and numbers to an extent that is highly objectionable from the grazier's standpoint. Fire, in contrast to grazing, kills the shrubs but does not injure the grasses when these are aestivating. On areas where the grasses have not been too severely depleted, it has been demonstrated that the forage production can be increased tremendously by burning to kill the shrub, then not allowing grazing for a few years until the grasses have multiplied to form a complete cover (Fig. 88). Sagebrush eventually returns to such an area, but this is so slow a process that burning need be repeated only at intervals of many years. Obviously, if grazing has already removed all peren-



Fig. 88. In the distance is unburned sagebrush-grass vegetation. The area in the foreground was burned three years before the picture was taken. Fire has eliminated the sagebrush temporarily and allowed the fire-tolerant grasses to become dominant. Dubois, Idaho.

nial grasses, burning must be followed immediately by artificial reseeding to secure a stand of desirable grasses.⁴⁸

It is generally true that fire favors grass at the expense of woody vegetation, and other examples in addition to the above can be cited. Grass fires set by the aborigines were responsible for extending prairie eastward into the winter-deciduous forest in the region centering about eastern Iowa.²²⁵ In New Zealand even rainforest has been converted to grassland by means of burning.³⁹⁵

Fire is recognized as an important tool of forest management on the Atlantic Coastal Plain of southeastern North America.²¹⁴ Here pines, especially *Pinus palustris*, are relatively fire-tolerant and valuable in comparison to the relatively fire-sensitive and worthless oaks. Light surface fires at intervals of a few years are sufficient to keep oaks entirely eliminated, yet the intervals are long enough to allow the pines to germinate and attain a size sufficient to withstand burning. Temperatures during these fires usually remain below 100° C, and the maximum is sustained for only a few minutes, so that humus is not charred and the net effect of burning is beneficial to the soil in this region.²⁹² Fire has no significant effect on the growth



Fig. 89. Fire-maintained stand of *Pinus palustris* near Baconton, Georgia. Burning has kept out oaks but has not been so frequent but that a few pines have become established recently. The trees are being bled for resin.

of pines large enough to survive burning, and, because grasses thrive under these conditions (Fig. 89), both timber and forage resources are better under burning at intervals of several years than under complete protection or under annual burning. In the Rocky Mountains fire can be used on certain habitat types to thin over-dense young stands of *Pinus ponderosa*.⁷²⁵

Agronomists too have made some use of the selective effect of fire to favor desired plants by the technique of *flaming*, which is applicable with intertilled row crops such as cotton and sugar cane. Weeds are controlled at first by the usual cultivation, but after the crop plant is tall enough so that its leaves are well above the ground (15 cm for cotton) a tractor-drawn machine throwing jets of flame is used to kill weeds. The flame is low and horizontal, and is controlled carefully so that weeds less than 5 cm tall are killed without injuring the crop. Flaming must be repeated often enough so that weeds will not grow beyond the vulnerable seedling stage.

Use of Fire to Improve Quality of Forage

Deer, elk, and moose depend heavily on browse provided by shrubs and tree seedlings, especially in winter after the foliage of deciduous woody plants and herbs has withered or become covered with snow. Unless these plants are browsed excessively they tend to grow too tall for the animals to reach the nutritive younger twigs. On sites where game is more valuable than trees, occasional burning of patches of vegetation is recommended so that new sprouts from the roots will renew the supply of available browse.⁶³⁵ Not only are the young twigs more available, but they are more nutritive than twigs from older plants.^{165, 185} In certain grasslands also an improvement in nutritive quality is among the benefits resulting from occasional burning.⁵⁵⁵

Use of Fire to Remove Undesirable Organic Debris

The greater the amount of dry litter, the hotter and more devastating a fire is. Under certain circumstances the cumulative effects of occasional small fires are not so destructive as the holocausts that would almost certainly result from fires coming at greater intervals.^{181, 214, 421}

Insects and fungi that are facultative parasites often must live in plant debris for a period until conditions become propitious for

attacking living hosts. As suggested above, whenever the potential hazard of such organisms outweighs the value of the plant debris as a source of humus, sanitation by burning is desirable. Many agricultural situations demand the burning of crop residues that harbor such pests as pea weevil, the European corn borer, cinch bugs, viruses, rusts, smuts, and rot-producing fungi.²⁷⁵ On the Atlantic Coastal Plain one of the benefits of burning the pine forests is the control of the brown-spot needle disease of *Pinus palustris*.

In other regions the benefits of periodic burning may lie in the destruction of ticks and other important parasites of animals. Fire is quite effective in reducing the numbers of tsetse flies in Africa.

The seeds of many plants germinate and become established better in contact with mineral soil than with superficial layers of organic debris. Organic debris exhibits wider fluctuations in temperature and moisture, and it holds seeds suspended so that they cannot make direct contact with the mineral soil. For these reasons controlled burning has a place in the silviculture of certain trees by preparing the land for planting or natural seeding.

Logging operations invariably leave the forest littered with unmerchantable logs, tops, and branches, which are collectively called "slash" by foresters. This material becomes a fire hazard as it dries out; it may be detrimental to the establishment of seedlings of the next generation of trees, and it may harbor injurious pests. On the other hand, the debris improves soil structure and fertility, reduces erosion, and under other circumstances may favor seedling establishment. Depending on the relative significance of these factors under different conditions, silviculturists recommend piling and burning of slash, scattering it uniformly and burning, or scattering and letting it decompose gradually in the hope that it will not catch fire.⁵¹¹



CHAPTER NINE

The environmental complex

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The preceding chapters have considered, as far as possible, the separate influences of soil, water, temperature, light, atmosphere, fire, and other organisms on the plant. It is now desirable to focus attention on the important fact, which has previously been suggested in many places, that factors never operate separately or constantly upon the organism, that environmental relations are at once complicated and dynamic.

When ecology was in its infancy as a science, a disgruntled wag characterized it as "the painful elaboration of the obvious." But as more and more information accumulated, exactly the opposite viewpoint had to be accepted—what seems obvious superficially, involves

complexity that it at times staggering. It is the purpose of this chapter to point out the main phenomena responsible for this complexity.

ECOLOGIC VERSUS NONECOLOGIC BEHAVIORISMS

Plant behaviorisms can be divided into three categories. One group comprises those which appear not to be responses closely related to environmental stimuli. For example, the cessation of cambial activity in many temperate zone trees cannot be related to concomitant changes in seasonal weather conditions. Apparently a cycle of physiologic activity is involved that runs its course, its termination being essentially endogenous.

A second category of behaviorisms are those "triggered" by some environmental condition, and once the process gets under way it does not depend on a continuation of the stimulus. Thus a fraction of a second of exposure to light initiates the germination process in *Nicotiana tabacum*, but once illuminated even so briefly, germination continues even in darkness.³⁴⁵

Finally, there are responses that are induced and sustained by some environmental condition, ceasing when the condition is removed. The appearance of ephemeral leaves on the desert plant *Fouquieria splendens* exemplifies this situation, for the small delicate leaves appear whenever growth water becomes available, then are abscised promptly when the wilting coefficient is attained.¹⁰²

The nature of the first of the above three categories of behaviorisms sometimes suggests possible ancestral ecology under which the phenomenon had survival value. For the second category, ecologic explanations involve threshold values on factor gradients, with all but one environmentally conditioned process being completed. The third category is the most obvious, and by the uninitiated is assumed to be the only type of behaviorism.

Behaviorisms then may not always be related to present environment, and sometimes may even lie largely outside the realm of ecology.

MULTIPLICITY OF FACTORS

The complexity of vital processes within the organism is far more generally appreciated than the complexity of environmental media

which surround the organism.³⁸⁸ We commonly report specific germination percentages for a given lot of seeds, yet the value obtained has been governed by genetic differences in the taxon from one population to another, by the year of collection, stage of plant development, weather preceding collection, methods of cleaning, storing, and testing, date of testing, etc.³⁸⁵ In the glass-house we usually assume far greater uniformity of environment from place to place than can be verified by testing, with the result that critical work there demands a systematic rotation of pots.³⁸⁶ Furthermore, biologists are continually discovering wholly new aspects of environment which have had strong but unappreciated influence on their observations, as attested by the lateness of the discoveries of photoperiodism and thermoperiodism. Apparently some of the contradictory results of different experiments may have been only a consequence of working under different intensities of smog, which was exerting an unrecognized influence upon plants.⁷⁴⁰ How many experiments have been performed and close interpretations drawn without knowing that the mere handling of leaves may cause a large increase in their subsequent rate of respiration!²²⁷

A plant is at once affected by the amount of heat, light, moisture, and nutrients available to it, by the degree of activity of parasites and mycorrhizal fungi, etc. The fact that its life processes continue under the numerous and fluctuating elements of environment bespeaks a considerable breadth of tolerance of environmental variation. Yet this tolerance is not unlimited. When the intensity of any one of these factors begins to tax the plant's ability to cope with it, vigor declines, but because of the multiplicity of factors involved the cause of the disturbance is often unapparent, becoming known only after a series of experiments have been directed toward this end.

This situation is pointed up by the problem facing a botanist who is called upon to ascertain the cause of death of a plant. If a parasite was responsible it may have left definite and recognizable symptoms in the form of necroses, galls, etc., but not all parasites do this. On the other hand death may have resulted from any of a wide variety of nonbiologic factors, and in this group also symptoms vary from the manifest to the obscure.

Because numerous factors are always operating on the organism simultaneously, each function is a multiconditioned process. Perhaps no better illustration of this fact is provided than that furnished by the research connected with the Neubauer technique for determining the availability of P and K in soils. Some time ago it was sug-

gested that if a number of rye seedlings were grown in a definite quantity of soil mixed with a definite quantity of sand, and the seedlings were subjected to chemical analysis after about two weeks, the amounts of P and K in the ash would provide a standard measure of the availability of these elements in the soil used. However, subsequent research has shown that mineral uptake is not only affected by the chemical nature of the soil solution (as hypothesized), but by temperature, by soil moisture, by light, and by the degree of change in soil texture brought about by incorporating sand.¹¹ Because so many factors affect plant functions, the method is valid only when a series of soils are tested simultaneously and all groups of plants are subjected to identical conditions except those of soil nutrition.

Environment is highly complex and integrated, but this should not be a matter for despair, for environments are probably still less complex than organisms!

HETEROGENEITY OF ENVIRONMENT

The concept of habitat implies only a portion of space that is characterized by certain temporal and spatial variations in factor intensities. There may be a close similarity in the combinations of conditions obtaining among the members of a class of habitat (e.g., the dune habitat), but the conditions within each of the habitats, especially of light, moisture, and temperature, vary considerably from place to place.

The problem of measuring those physical conditions that really govern plant behavior is much more difficult than is commonly conceived. For example, when an investigator correlates the records made by a battery of weather instruments with the growth of a tree near by, cause and effect are really not under study. The results, if positive, show no more than a relationship existing between certain atmospheric and certain protoplasmic phenomena, all of which are members of a galaxy of changes set in motion by unmeasured master forces. Actually only a thin shell of environment adjacent to the organism is of immediate causal significance, and the conditions in various parts of this shell differ materially from the conditions to which the instruments in the weather station are exposed.²⁵

Environmental factors are subject to marked vertical stratification, so that the axis of the average terrestrial plant extends through sev-

eral distinct *microhabitats* or *partial habitats*.⁷⁶⁰ The questions might be raised: When rising temperatures in spring allow a resumption of growth in a tree, are the edaphic or the aerial aspects of temperature the more important? How are we to evaluate the different levels of temperature stratification in each? The temperature of the meristematic tissue seems to be the datum of maximum value here, for air temperature as recorded in the instrument shelter is no more than a second temperature condition dependent indirectly upon solar radiation. Yet, if the growth of one organ is conditioned by hormones produced in another, we cannot single out the temperature of the apical meristem as the only temperature condition affecting its activity! Questions of this sort cannot be solved at present, but ecology has at least advanced far enough so that the problems have been recognized.

Environment can be sampled from the standpoint of the various microhabitats surrounding the different parts of a large plant, or from the broad standpoint of variation in homologous microhabitats within an area of essentially uniform plant cover. When the latter is the objective a great number of records is necessary in order to obtain both a mean value capable of reproduction and a true record of the extremes. Useful information concerning variability can often be obtained by sampling the environment at fixed intervals along a line. When only a few instruments are available they can be moved about at regular intervals over the area under study, one being left in place as a standard of comparison for the others.⁷⁵²

The importance of microenvironment is emphasized by the modern trend in agronomy and soil conservation, as exemplified by the individual consideration given in land-use planning to each part of a farm. The interplay of variations in microclimate and soil results in significant variations in agricultural potentialities within short distances. At some places windbreaks are beneficial; at others contouring and wide spacing of plants are desirable to increase precipitation effectiveness; and at still other places drainage or the planting of shallow-rooting crops is advisable.

Another aspect of this problem of environmental heterogeneity involves the fact that variations in the supply of light or moisture become relatively widest at places where the quantities of either are least. Not only are the variations widest here, but also the plant is more sensitive to them, and therefore the same quantitative aspects of environment must be evaluated by different standards in different habitats. At the dry edge of a species' range small variations in

moisture are very important in its local distribution, whereas at the cold edge of its range small variations in temperature become critical. Near its center of distribution the individuals of a species commonly appear to be insensitive to even wider absolute values of either moisture or temperature.

DYNAMIC NATURE OF ENVIRONMENT

In the natural course of events, identical combinations of environmental conditions are repeated only at rare and irregular intervals.³⁰⁸ The intensity of most factors varies with the hour, day, and season, and the *rates of change*, the *durations of particular intensities*, and the *extreme values* are all ecologically important aspects of the same environmental condition. Examples of the importance of these aspects of environment have been provided by earlier discussions of temperature, tides, daylength, etc. Also it has been pointed out that the common practice of integrating measurements taken over a period of time as mean values may obscure very important time aspects of factor variation.

Seedlings are especially vulnerable to the vagaries of environment, and this is undoubtedly reflected in the frequency with which species have evolved the habit of intermittent germination, with respect to the seed matured at any one time. The importance of extremes for seedling establishment is also shown by populations of perennials that are made up of only a few age classes. These plants, especially on suboptimal habitats, produce a successful crop of seedlings only as a result of a rare concomitance of extremely favorable conditions.

Because of the rapidity with which factor intensities change, the stimulation of protoplasm often does not find expression in form and function until after the condition that set it in motion has passed. Therefore plant behavior is to no small extent dependent on preconditioning. For example, vegetative and fruiting vigor are frequently dependent on physiologic preconditioning during the preceding winter. A morphologic type of preconditioning is illustrated by leaves which, though formed during a favorable season, are dwarfed as a result of dependence on inefficient xylem which was produced during the preceding dry season.²⁹¹ In *Pinus resinosa* terminal growth of the stem was found to strongly reflect conditions of the preceding season, although cambial growth and needle elongation are more strongly influenced by current weather.¹⁷²

In the alga *Scenedesmus quadricauda* variable relationships between population growth and the P content of the medium appears to be largely a result of the organism being able to accumulate this nutrient above current needs when it is plentiful (a phenomenon called "luxury consumption"), then to draw upon the cellular store for several weeks after the external supply of P has been cut off.⁵⁰¹ Even the seed reserves of minor elements such as Mo may be sufficient for completing the life cycle of the plant developing from that seed.²⁸⁹

Delayed effects of environment can be even less direct than those illustrated by the above phenomena. During exceptionally dry seasons plants in arid regions exhaust soil moisture to exceptional depths, thereby increasing the amount of precipitation necessary the following year to bring moisture levels and consequently plant growth back to normal.⁴⁷⁹

The above phenomena involve short-time fluctuations in factor intensities, some of which are rhythmic, others of which recur at irregular intervals. Another class of environmental variations involves unidirectional changes that take place over a series of years, as for example when an abandoned field is allowed to revert to native forest. During this process a drastic change is brought about as the warm sunny habitat is converted into a cool and shady one. Only after the lapse of several decades when the native forest approaches maturity does further evolution of the habitat slow to an imperceptible rate.

Finally, in addition to the recurrent and the evolutionary types of environmental change discussed above, there is a third which may be called the ontogenetic type. The microenvironment of the tiny seedling is usually quite different from that of the developing organism, and the mature plant comes under the influence of still other parts of space. Thus habitat change is incurred simply through the increase in size of a plant.⁷⁶⁹

VARIABILITY OF PLANT REQUIREMENTS

Ordinarily the combination of factor intensities most favorable to the welfare of a plant differs at different stages of the life cycle. Examples of this variability of plant requirements are numerous. The seeds of certain bog-inhabiting trees find conditions most favorable for germination on habitats that are distinctly too wet for the best growth of the mature trees.³⁸⁹ In peas, growth has been found to be

most closely determined by temperature during the early stages of the life cycle, but later light becomes the most important single factor.⁶⁶ Wheat is completely drouth resistant until the coleoptile is 3 to 4 mm long, after which it becomes increasingly more sensitive to dryness.⁴⁶¹ A plant may require a special sequence of photoperiods to pass successfully through different stages of its life cycle. Also temperature requirements are usually lower for breaking dormancy than for germination, and germination requirements are lower than those for normal vegetative growth; vegetative growth requirements in turn are often lower than the most suitable temperatures for flowering and fruiting. During its annual cycle of development, the optimal temperature for *Tulipa* bulbs varies from 8 to 23° C. It is obvious that all environmental requirements of the different functions at each stage of development must lie within the seasonal variations which prevail during that stage of development. Generally the period of seedling establishment is the most critical for the average plant. Either earlier as a dormant seed, or later as a well-established individual, it is capable of withstanding conditions to which the seedling would succumb immediately.

Not only do temperature requirements vary throughout the year, but at any one date different organs and even different tissues of the same organ may respond differently to temperature. Examples mentioned earlier are the destruction by frost of the gynoecium while the surrounding floral parts remain uninjured, and the killing of the youngest xylem cells while the enveloping cambium escapes damage. Thus even one plant does not behave as a unit. Consequently in experimental work it is usually essential to draw comparisons only between exactly the same portions of homologous organs of equal age.⁷¹⁰

Genetically determined variation from plant to plant within one experiment becomes a problem necessitating replication in proportion to variability, largely so that average differences will reflect treatment more than genetic differences. A better means of overcoming this difficulty is to use plants that can be propagated vegetatively, so that replication becomes desirable chiefly as an insurance against accident. Genetic uniformity is quite high in named varieties of cultivated herbs that are grown from seed, but one can seldom solve problems in the ecology of one species by using another as the subject for experimentation.

Another aspect of this problem, and one that frequently has a strong effect on conclusions in experimental work, is a phenomenon

that has variously been described as fatigue, protoplasmic adjustment, physiologic conditioning, or simply the time factor. It has often been observed that the new pace taken by functions when environment is changed abruptly does not usually persist for long. After an initial change in one direction, a secondary change usually sets in in an opposite direction, although the second change is less than the first. Thus, when a plant is placed under more favorable temperature conditions, its rate of growth may be speeded up to a degree which it cannot maintain for more than a few hours. Most graphs in which the rate of functioning is plotted against time are curvilinear rather than rectilinear. When given sufficient time for adjustment, plants can become adapted to a surprisingly wide range of environmental variation, but the time element is very important, and adjustment must be brought through gradual change in environment or the plant suffers heavily.

FACTOR INTERACTION

It is a commonplace in ecology that one factor compensates for deficiencies in another.⁵⁶⁹ A high water table, or an abundance of fog, or low temperature, each may compensate for low rainfall. Light influences plant requirements for nutrients such as Zn¹⁹⁶ and K, and there is good evidence that the effect of every nutrient element in the soil depends to a certain extent on the quantity of other elements present at the same time.⁴¹⁵ Dry climate may compensate for the lack of bumblebees to pollinate red clover by so reducing the size of the flowers that smaller bees can perform this function. Apparently the wide range of environment tolerated by many species is attributable at least in part to the fact that deficiencies in one factor may be compensated for by others as they arise. The same ecologic sum can be derived from different combinations of individual factor intensities.

Plants may become predisposed to one injurious factor by being exposed to another. Frequently a plant succumbs to parasites only as a result of debility incurred by growth under unfavorable climatic or soil conditions. But sometimes the reverse is true, the plant being subject to parasitism only when conditions favor lush growth.

It has often been noted that the separate actions of two factors do not have the same influence where they are combined. For example, in one fertilizer trial the addition of NaNO₃ increased yield 10%, and in another trial the addition of K₂SO₄ had the same amount of in-

fluence on yield. But when both were added, the increase was not 20%, but 100%!⁴⁶

Extrapolation is also dangerous where one might wish to predict a certain ecologic relationship basing the prediction on experimental work performed at a remote location, for climate exerts a strong control over the plant's requirements for nutrients, water, energy, and resistance to parasites, salinity, flooding, and other injurious forces.

Because environmental factors are interrelated and dynamic, and because they often exhibit delayed effects, an alteration of one factor frequently initiates a series of adjustments of far-reaching and often unpredictable consequences. Thus an experiment in fertilizing forest soil resulted in increasing the density of the tree canopy, which in turn had a marked effect on the epiphytic flora.

A particularly difficult problem is posed by groups of factors that are inseparably related. Thus heat, light, and moisture relations vary simultaneously with every change in the intensity of solar radiation, and a number of soil characteristics always vary with change in pH. In these instances it is very difficult to design experiments to show the relative effects of different phases of the factor complex.

A difficulty of experimental ecology not encountered in physical or chemical work is the change that a plant undergoes when it is subjected to different conditions. If in a photosynthesis experiment one plant is grown under bright light and the other in shade, with all other factors equal, the morphology and physiology of the sun plant will soon become so modified that one is no longer following the safe rule of comparing systems differing by a single component. He will be comparing the photosynthetic rate of *thick leaves* under *bright light* with that of *thin leaves in shade*.⁴⁷ This problem cannot be solved by growing plants under identical conditions and then suddenly transferring them to the experimental conditions, for the responses thus obtained may be so abnormal as to lack true ecologic significance.⁴⁸

The above facts show that not only are the factors of environment interrelated, and the functions within the organism interdependent, but the two complexes are practically inseparable. Another phenomenon which obscures the line of division between organism and environment is that for a limited time environmental deficiencies can be compensated for by adjustments within the plant. Thus, the characteristic effects produced by the permanent wilting percentage of the soil are postponed in a succulent plant by a redistribution of water contained in the succulent tissues.

Because so many experimental data of the above nature have accumulated, it is now clear that mathematical expressions of the relations between environment and response are of value only as an aid in the interpretation of field observations. Another reason why the concept of definite tolerance limits has had to be depreciated is that most species are not genetically uniform. Instead, they are composed of races many of which are indistinguishable except for physiologic tolerances. This point will be discussed in detail later. For the two reasons just stated, field ecologists attempting to explain plant behavior are often forced to confine themselves to inductive methods, seeking to establish concomitance between behavior and environment, and realizing that the phenomena may never be capable of expression in any but broad generalities.

An awareness of the inextricable interrelationships among all the physical factors and all the organisms of a particular habitat has led ecologists to recognize the ecosystem as a natural unit in the study of landscapes. This is not taken to imply that meticulous study of one ecologic relationship is undesirable, but that its meaning is enhanced a great deal when the results are viewed against a background of the biophysical complex of which it is a part.⁷⁵¹

OPTIMA AND LIMITING FACTORS

Enough has been said above to show that a fixed optimum intensity of any one factor does not exist. For every change in one factor, a different optimum of all other factors comes into existence. The concept of optimum is further complicated by the fact that optimal requirements differ for different processes in the same organism. Thus it is clear that when the term optimum is used it should always be understood that "apparent optimum" with respect to one type of response is really implied.⁹ Optimum conditions for longevity (resulting in trees reaching an age of 4,100 years) depend on suboptimal conditions for nearly all plant functions!⁵⁸⁹

A plant extends its range in all directions until some detrimental aspect of environment prevents a completion of the life cycle either by vegetative or sexual means. As one aspect of environment approaches the extreme limit of tolerance, the welfare of the plant comes to depend closely on this condition, and the expression *limiting factor* is used. For example, where forest abuts a dry grassland region, trees become confined to habitats that have a water-balance

less severe for them, suggesting that moisture deficiency is the primary environmental limitation. In this way the behavior of plants at the edges of their ranges usually provides valuable clues to the most important factors limiting distribution. However, there is a definite danger in attaching too much importance to apparent limiting factors (Fig. 90). For example, at the dry timberline referred to above, rainfall would cease to be inadequate if temperature were lowered, and possibly neither temperature nor precipitation would have to be altered to allow forest extension if herbaceous competition with tree seedlings were eliminated. Therefore, the term limiting factor must usually be defined as the factor of most immediate importance in the existing biophysical complex. The concept is justified in that often one can remove the limitation by a single act. Thus trees will usually grow in a dry region either if irrigated, or if clean cultivated so as to eliminate competition from other plants. Similarly, on sandy outwash in New York the poor growth of trees can be corrected merely by fertilizing with K,²⁷⁸ and dormancy can often be broken by altering temperature alone.



Fig. 90. Although wind is the most evident factor operating at this natural edge of the forest, the immediate cause for the difference in vegetation appears to be edaphic. Forest is confined to areas where a layer of silt overlays the gravelly substratum. San Juan Island, Washington.

Liebig's law of minimum, that the size of a crop is determined by the essential nutrient that is present in minimal amount, does not apply to environmental relationships so regularly or so closely as might be expected. Sometimes factor compensation mitigates the effect of a severe environmental condition without lessening its intensity, whereas at other times or places the same condition untempered by compensation would have a much stronger effect. Another possible explanation of exceptions to the law of minimum is as follows. Optimum environment demands the most favorable levels of all factor intensities; therefore an improvement in any single environmental condition, even if it is not the most detrimental one, tends to favor plant growth.

Since Liebig was interested only in nutrient deficiency, whereas excessive amounts of nutrients and other aspects of environment may be equally critical, and whereas plant success is conditioned by the concerted action of all factors, a much broader restatement such as the following is needed. The more nearly a factor approaches the extreme condition tolerated by the individual at a given stage of its life cycle, the greater the relative impact of change in that factor on plant behavior. This implies that wide variations in factor-intensities are of relatively little consequence in the region of the optimum.

THE ECOLOGIC VIEWPOINT IN EXPERIMENTAL WORK

Because the living organism is an integral part of the cycles of matter and energy, and because there is a continual exchange of materials between the organism and its environment, life and environment must be considered together. They can be divorced legitimately only as a matter of temporary convenience in experimental work, and even here definite precautions must be taken if the results of study are to find application.

In an endeavor to understand the physiologic roles played by different factors, biologists have long employed the method of controlled experimentation in which the responses of paired individuals are compared when only one factor in their environments differs. Such experiments, though they are basically valid and may yield information of considerable value in understanding the relations between organism and environment, are often performed under conditions that produce results of little or no practical significance. The investigator must take into account the fact that all conditions that

differ significantly from those obtaining in the natural habitat may affect his results, even though experimental and control plants receive the same treatment. This situation stems from the fact that each plant has become adapted to a particular combination of factors which, though they may vary, do so in a definite rhythmic pattern, remaining within certain set limits and maintaining definite relationships. A potted plant suddenly changed from cool to warm constant-temperature chambers, then back again, with the purpose of simulating diurnal temperature rhythms in the field, is subjected to unnaturally harsh conditions, especially if roots and shoots are maintained at the same temperature levels.⁴⁸¹ Even in the field, soil temperatures, though cooler than air in summer, frequently appear to rise above optimum levels for root growth, so that in controlled environment the soil should be kept cooler than air.

Whenever a plant is forced to grow in an unnatural environment it cannot be expected to exhibit normal responses to individual factor variations. Therefore the results of laboratory experiments must always be applied with caution to plants growing in the field.^{47, 148, 602, 770} Plant responses as observed in the greenhouse may actually be reversed in the field!^{70, 117, 282, 413, 464} When the problem is one in theoretical physiology, artificial environments are satisfactory, but, where practical ecologic application is to be made of the data, artificial environments may yield very misleading results. In ecologic experimentation, the more closely natural conditions are simulated the more applicable are the results.

An example of a potential source of error common in experimental work may serve to clarify the above discussion. When plants are grown in small containers their root systems are crowded and the major portion of the absorptive system is usually located around the outside of the soil mass next the container. In this position the sensitive yet important rootlets are very susceptible to drying out in unglazed pots, or to killing by overheating in metal containers that are not shaded constantly, or at the very least they are subjected to temperature conditions far different from those encountered anywhere in the field. Unless these relations are fully recognized and the dangers circumvented by adequate precautions, experimental results are as likely to be affected by this factor as by the condition that is the intended object of study.²¹¹

The value of any careful experimental work depends on the probability that essentially the same results would be obtained if the experiment were repeated. Therefore, it should be clear from all the

preceding points discussed in this chapter that complete and accurate results of all measurable factors should be published with any experimental results for the latter to be of maximum utility. This usually involves far more information than the investigator realizes.

THE PHYTOMETER METHOD

The above discussions of the complexity of environment and of plant responses emphasize the inadequacy of instruments that measure single factors like wind and temperature. Even when accurate records of all known transpiration-promoting factors are available, we do not know how to evaluate them in order to predict transpiration rates. Nor can the photosynthetic rate be predicted when all measurable factors are known.⁶⁰²

The net influence of a particular environment on the plant is expressed most precisely in the responses of the plant growing in that environment. Consequently the theoretically ideal instrument to evaluate environment in terms of plant growth is a series of plants which are grown in different habitats in order to observe differences in their structure, behavior, or chemical composition. Such experimental plants, or pieces of low vegetation transplanted intact, are called *phytometers*.¹²⁴ These not only have the advantage of integrating all factors, but also they overcome the problem presented by the fact that instruments are frequently more sensitive to variations in single factors than is the plant on account of the ability of protoplasm to make adjustments. Obviously the plants in the series should be genetically as nearly identical as possible; error due to variability may be reduced still further by using sufficient replications to permit a biometric analysis of results. Phytometers should always be accompanied by adequate batteries of instruments so that quantitative relationships can be established between stimulus and response.

Perhaps the most frequently overlooked limitation to this method lies in the fact that no two species react in exactly the same way to a given set of environmental conditions; therefore the behavior of one species cannot be used to prognosticate the behavior of another on the same series of habitats. Also, the fact must be taken into account that, when additional growth is used as a criterion of effectiveness of habitat factors, the amount of new growth is conditioned by the initial size of the organism as well as by environment. Thus it has been observed that the larger the seed the greater the size of

the seedling after a given period of development with this effect sometimes persisting into the second year.⁵⁰⁰

In North America the widest practical application of the phytometer method has been made by foresters who have used the average rate of height growth of a particular kind of tree as a criterion of the productivity of different habitats for lumber of that species.

IN CONCLUSION

The ecologic approach involves a struggle for perspective which is easy to underestimate both as to importance and complexity. A realization of the multiplicity of interacting factors and the complexity of plant requirements constitutes one of the two most profound biologic principles that has been contributed by autecologic inquiry. The second will be discussed in Chapter Ten.



CHAPTER TEN

Ecologic adaptation and evolution

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ADAPTATION

Any feature of an organism or its parts which is of definite value in allowing that organism to exist under the conditions of its habitat may be called an *adaptation*. Such features may insure a degree of success either by allowing the plant to make especially full use of the amounts of nutrients, water, heat, or light available to it or

by bestowing a significant amount of protection against some adverse factor, such as extremes of temperature, drouth, or parasites. By accumulating adaptations, organisms utilize the earth's resources ever more efficiently, and after eons of development a great many if not most of the characteristics of each species are adaptive. In fact, it has been said that an organism is "a bundle of adaptations."

Conspicuous adaptations, such as those of carnivorous plants and entomophilous flowers, are perhaps too well known, for they tend to distract attention from inconspicuous but far more numerous adaptations that are to be found everywhere. For example, radial symmetry is particularly appropriate for plants whose moisture, light, and nutrients come from all directions. Likewise, because the absorption of CO₂ by the shoot and water by the root are largely conditioned by the amount of absorptive surface presented, profuse branching of both root and shoot is advantageous. Light penetrates only a short distance into tissues; therefore the prevalence of broad, thin photosynthetic organs throughout the phyla is of significance. The drier or colder the climate, the higher is the osmotic pressure of plant saps,²⁰³ and the colder the climate, the greater is the calorific value of plant fats.⁴³⁸

It has been noted that although plants are in general well adapted to the quantity and quality of energy received from the sun, their CO₂ optimum is much higher than that contained in the air. This has been interpreted as indicating that the atmosphere during the evolutionary emergence of modern plants was higher in CO₂.

In addition to such general types of adaptations, special habitats are often accompanied by plant characteristics (succulence, aerating tissue, etc.) that seem of value there. Since the possible means of adaptation to a particular type of environment are not many, taxonomically diverse species may follow converging lines of ecologic adaptation. Thus under desert environment the stem-succulent habit has arisen independently in the Cactaceae, the Euphorbiaceae, and the Asclepiadaceae. These groups retain many of their ancestral characters, especially reproductive structures, even though developing many physiologic and morphologic traits that are similar and bear the same relationship to desert environment. The principle is further illustrated by the root tendrils of *Vanilla* as compared with the ecologically equivalent stem tendrils of the grape, and by aerenchyma as compared with lacunar tissue in various emergent hydrophytes.

It often happens, however, that a single kind of adverse circum-

stance is met by entirely different types of adaptations which have equivalent value. An excellent example of this is provided by the divergence in physiology and morphology exhibited by desert plants. Here plants with very evident morphologic adaptations grow among others that lack visible manifestations of adaptations but rather are possessed of the necessary physiologic requirements to make their existence possible. Thus adaptation may be purely physiologic, as illustrated by resistance to disease, host preference among parasites, degree of palatability to herbivores, endurance of desiccation, etc. What appear to be purely morphologic adaptations are illustrated by sunken stomata, special pollinating mechanisms, form of shoot, etc. In reality there is much less difference between strictly physiologic and morphologic adaptations than is apparent, for a morphologic feature is but an expression of physiologic processes otherwise unevident.

Morphologic characteristics should always be subjected to physiologic experimentation before they are classified as having survival value, for interpretations of the physiologic significance of morphology based on human logic cannot be relied upon. It was pointed out, for example, that water may be transpired faster through the thick cuticle of one plant than through the thinner cuticle of another.⁵²⁸ Wherever morphology and physiology tell different stories, as in this instance, physiology must provide the correct answer, because morphologic features are assumed to have significance only as far as they influence the physiology of an organ. It is not a particularly comforting fact to note that most statements regarding the merits of assumed adaptations are unsubstantiated by physiologic tests.

All physiologic processes in plants are affected by the supply of water, heat, nutrients, and light. It follows that each plant must be fairly accurately adjusted to its habitat, at least in that it surpasses certain minimum adaptational requirements. To be perfectly adapted a plant would theoretically have to make the fullest use of the available energy and nutrients. It is significant in this connection that the crop plants with the highest carbohydrate production do use nearly all of the favorably warm season. Much of agronomic practice is directed consciously or subconsciously toward fitting the life cycles of crop plants into the prevailing climatic regimen by varietal selection, proper choice of planting dates, irrigation, protection against unseasonal frosts, etc. In these ways natural deficiencies in adaptations are compensated for.

Adaptation at first appears to be a process constantly conferring benefits on organisms. However, in the long run it is frequently disastrous as proved repeatedly by the paleontologic record. Where adaptation steadily pursues a given course without interruption it may eventually lead to such a high degree of specialization as to make survival absolutely dependent upon the maintenance of the environmental complex by which adaptation was guided. The trends of specializations in pollination illustrated by *Yucca* and by the Smyrna fig provide examples of this.

ORIGIN OF ADAPTATIONS

The correspondence between structure and function, and a particular habitat, obviously is not fortuitous. Man has long been interested in explaining how these adaptations came about, but until quite recently the interpretations have been almost entirely philosophical and not based on a careful analysis of facts.

The Older Viewpoint: Anthropomorphism and Teleology

Early ecologic thought was dominated by *anthropomorphism* and *teleology*. Anthropomorphism is the habit of attributing human characteristics to nonhuman objects, as in the expression that a plant "avoids" acid soils. Teleology is the doctrine that adaptation is purposive, as is implied in the statement that the wing of a seed is "for" wider dissemination. It was assumed that such an adaptation arose in response to a particular need, and indeed many phenomena superficially appear to warrant such an hypothesis. For example, root hairs, cuticle, and cork ordinarily do not develop on organs grown under water, and at the same time other tissues become modified in such a manner as to favor aeration. However, close analysis reveals that not all responses of plants to environmental stimuli are beneficial, and experimentation has shown that many responses, whether beneficial or detrimental, can be explained on a physical or chemical basis. Thus there is more evidence in support of mechanism than of vitalism.

The change away from the old viewpoint has been so recent, however, that scientific writing of high calibre still contains such terms as "food storage" and "calciphile." In general the continued use of such expressions is condoned for the sake of convenience or cus-

tom, for the older viewpoint has been thoroughly discredited. Precise expression would of course demand the substitutions of expressions such as "food accumulation" and "calciphyte" for the expressions mentioned above.

The Newer Viewpoint: Genetic Variation and Natural Selection

Most adaptations are now believed to arise by the selective action of environment operating as a sieve on genetic variations, the origins of which are strictly matters of chance. Since not all variations are genetically fixed, it will be necessary at this point to distinguish between two major types of variation. It will be noted that the topic here is variations rather than adaptations, for many if not most variations appear to lack survival value and therefore cannot be considered adaptational.

Environmentally induced variations. (= ontogenetic, or somatic variations; = modifications; = acquired, or noninherited characters). When a series of genetically identical plants is grown in diverse habitats, it becomes apparent that, to a certain extent, the characteristics of an individual develop according to the particular habitat in which the plant grows.⁴⁴ The degree of plasticity and hence variation ranges from striking differences to only slight changes, depending on the hereditary constitution of the plant. Thus *Polygonum amphibium*⁴² and *Callitricha palustre* exhibit very different forms when grown in water and on land, and many less striking variations in structure and function have been enumerated earlier in connection with the supply of water, light, oxygen, salts, etc. Environmentally induced variations of a morphologic nature are acquired only as a result of continued exposure during a long portion of the life cycle, but physiologic adjustments may be brought about in a few days.⁴³

Such effects of environment are simply the inevitable results of reactions of the physicochemical properties of the protoplasm to particular combinations of factors. They are produced readily and remain in equilibrium with their corresponding environments indefinitely, but no permanent changes are induced and the process of modification remains reversible. Different species tend to react in similar manner if not in the same degree to the same stimulus, but this does not necessarily indicate more than a certain similarity in protoplasm from one species to another.

Frequently variations of this type are beneficial and may be classed as adaptations. For example, exposure to drouth induces drouth

resistance, chilling increases cold resistance, and unequal shading stimulates a bending toward brighter light. Le Châtelier's theorem can be restated to fit such biologic phenomena as follows: any intensification of an environmental factor tends to increase the organism's resistance to further intensification of that factor.⁴⁵³

However, not all environmentally induced variations appear to be useful. Such phenomena as the change in flower color with change in soil pH in *Hydrangea* and the response of the basis of bald cypress trunks to the lapping of waves seem best described as neutral. Still other responses to environment may result in considerable detriment to plants. For example, barrel cacti germinate chiefly in the shade of shrubs, but as they grow the stems lean toward brighter light until they topple over and die.³⁰⁸ Again, the tall weak stems produced by cereal crops growing under exceptionally favorable moisture and nutrient conditions render the plants very susceptible to lodging and therefore exemplify an at least potentially detrimental response to environment. Finally, the formation of galls clearly favors gall wasps at the expense of the host.¹²⁷

Genetically fixed variations. (= inherited characters). These are ordinarily irreversible and arise only by changes in the structure of genes,* rearrangements of genes within the chromosome framework, recombinations of genes through hybridization, or irregularities during mitosis or meiosis that change the number of chromosomes per cell. Large changes of this nature occur only at infrequent intervals, but it is quite likely that numerous small changes occur frequently and eventually become important because of cumulative effect.

The origin of genetic variations is subject to the laws of chance, but as the individual develops, the relative merits of the new hereditary materials assert themselves more and more with the result that survival, maturation, and reproduction are definitely not random. If the new character is detrimental the organism is less successful than others of its kind, and hence the change is not likely to be preserved. If the innovation confers an advantage upon the recipient, it has better-than-average chances of survival. Thus natural selection, operating on fortuitous genetic variations, tends to produce

* A gene is a unit of inheritance, actually a definite segment of a chromosome which, by interaction with other genes and the environment, governs the manifestation of some character of the organism. Genes occupying identical positions in homologous chromosomes are called *alleles*. Different alleles control the same character but may vary its expression.

new forms ever more closely adapted to the habitat. Mathematically it has been demonstrated that, if a mutation increased the chances of survival only 1%, it would become established in half the population in about 100 generations. This emphasizes the significance of sex, for without this a species would be unable to exploit useful mutations through recombination, although vegetative reproduction alone will permit the perpetuation of unmodified mutations, as horticultural practices testify abundantly.

Natural selection favoring characters that create the maximum harmony between organism and environment provides the only explanation for the countless instances of ecologic similarity among taxonomically diverse species.

Of the thousands of genes that govern the behavior of an organism, only one need change beyond a certain extent in order to disturb the synchrony of the various functions and thereby prove fatal. The vast majority of genetic variations are probably unsuccessful because the physiologic balance has been upset by the new combination of genes. Thus there is an internal requirement for harmony, in addition to the demand for harmony between the new gene complex and the environment. When viewed in this light the slowness of the evolutionary process becomes understandable.

The principle of natural selection cannot be interpreted to mean that all structures and functions of present-day organisms have survived because they have been beneficial. Many if not most genetic variations must be so inconsequential with respect to natural selection that they must be considered neutral, i.e., lacking either positive or negative survival value. The endless variety of blade shapes and venation patterns in leaves is not known to affect the function of these organs and therefore must have no different survival values. Likewise the night-folding of leaflets which are so common in legumes appear unrelated to the welfare of these plants. On changes of this nature the environmental sieve fails to act with a selective or discarding action, and thus neutral traits have a chance of being preserved.

Inconsequential characters, however, may be due to genes linked in the same chromosome with other genes that control small but important physiologic characters, in which event natural selection appears to favor characters for which man can rightly see no value. Such small and directly insignificant morphologic characters then become important to the biologist solely because they indicate the presence or absence of physiologic attributes that are of ecologic sig-

nificance.²³ This aspect of linkage deserves much consideration, for small morphologic characters, no matter how trivial they may seem to the taxonomic "lumpers," may provide invaluable criteria of the ecologic status of individuals. On the other hand it is definitely known that the genes governing slight morphologic differences may not be linked to those governing slight physiologic differences, so that the two types of variations can be independent.

From an ecologic standpoint, all trivial characters should be ignored unless they are accompanied by some physiologic character. Since its beginning the subscience of taxonomy has been concerned chiefly with the comparative morphology of sexual reproductive organs, but the ecologist is much more interested in the details of structure and function of vegetative organs, especially of juvenile stages, because of their significance in relation to survival. It is unfortunate that it is so inconvenient to recognize taxonomically such inherent differences among plants as the rate of seedling root penetration, time of flowering, etc., for these small physiologic characters are frequently important in determining failure or success.

There seems to be no doubt but that many attributes have been gained or lost in evolution simply as the result of chance mutations of neutral nature. It has been pointed out that, if adaptation by mutation is a random phenomenon unrelated to the organism's needs, warm-climate vegetation should contain species possessing cold-tolerance, for in warm regions a change in this direction would be neutral from the standpoint of natural selection. This has proved to be true, for many plants have been successfully transplanted into regions 10 to 30° F cooler than their native homes.⁷⁴⁴ Further evidence bearing out this conclusion is provided by the fact that in the floras of the tropics some species have come to require the short days that prevail there, whereas others are indeterminate in daylength requirements. Mutations from either one of these types to the other would be neutral, but those producing long-day requirements would be fatal.

Any mutation that gives the organism some characteristic of potential value, but which at the time has no survival value, may be called a *preadaptation*. For example, blight-resistant strains of species have been discovered in regions where the blight organism does not occur. Long-day-tolerant and cold-resistant species native to the warm tropics provide additional examples of preadaptation. This phenomenon may explain the fact that different species of the same habitat sometimes move into distinctly different habitats when

climates become more diversified.⁷⁴³ Thus, the paleontologic record shows that *Sequoia*, *Fagus*, and *Glyptostrobus* were members of the same forest in Miocene time, but with subsequent climatic differentiation each came to occupy a different climatic area.

The genetically fixed type of adaptation is the more advantageous where an early appearance of the character is essential in the life cycle, for the younger the organism the greater its sensitivity to adversity and the less time it has had to become conditioned to meet crises. It should be noted that the use of the expression "genetically fixed" does not mean that such characters are not susceptible of environmentally induced modification, for the effects of environment become superimposed on the effects of heredity as the seedling develops into a mature organism. In addition, somatic and genetic adaptation frequently parallel each other and can never be distinguished without resorting to experimentation.

FATE OF ADAPTATIONS

A perplexing problem which long confronted biologists is that certain structures and functions that appear to be definitely related to one type of environment are occasionally found in an entirely different environment. Examples of such paradoxical situations are provided by the xeromorphic yet hydrophytic pond pine (*Pinus rigida* var. *serotina*), by the succulent *Sedum ternatum* of the mesophytic winter-deciduous forest, by semiaquatic cacti, and by the functional nectaries of the parthenogenetic dandelion. As long as ecologic thinking was dominated by the assumption that an organism and its environment present a closed system of cause and effect, that each characteristic of form and function bears a direct relationship to habitat, phenomena such as these were indeed mysterious enigmas. However, when the truly scientific methods of reason and experimentation were substituted for the method of speculating upon non-experimental observations, and the dynamic natures of both organisms and environments were taken into account, it became apparent that the relations between organism and environment often become intelligible only when placed in historical perspective.

It is now believed that genetically fixed adaptational features frequently outlive their usefulness, and, as long as they do not prove definitely detrimental under changed habitat conditions, they may persist indefinitely, although they can no longer be called adapta-

tions. It would be a rare circumstance indeed if one gene change which allowed or demanded the movement of a succulent xerophyte into a mesophytic habitat were always accompanied by other gene changes which simultaneously abolished succulence and all other xeromorphic characters at the same instant. Plants have no ability to discard physiologic or morphologic features that are of no use to them. Constant selection pressure keeps essential structures and functions at approximately their peak of efficiency, but, when under changing conditions a structure or function becomes no longer essential, it merely becomes subject to atrophy through a lack of this selective maintenance. Thus essential functions may be in close adjustment with the present factor complex even though "obsolete adaptations" persist.

THE GENECOLOGIC CLASSIFICATION 288, 645

During the nineteenth century the fact became established that a species commonly includes genetically distinct races, but genetics itself had not yet been developed and little progress was made in studying this important phenomenon.

Beginning in 1920, Turesson assembled in an experimental garden at Akarp, Sweden, groups of 20 or more individual plants belonging to the same species but native to different parts of the species' range. Persistent differences among these groups growing in the same environment verified earlier conclusions that a taxonomic species is not a single ecologic unit but is composed of numerous races which exhibit inherent differences in physiology and often in morphology as well.⁶⁴ The races were observed to differ in earliness of flowering, height, erectness, thickness of leaves, etc., but none of these differences had been sufficient to warrant taxonomic recognition, and often they showed intergradation.

Turesson further showed that many of these genetic races are correlated with particular habitats, that one may be confined to sunny habitats and another to shade, some to alpine regions and some to lowlands, etc. Thus they are truly ecologic races. In other experiments he observed that, when plants similar in appearance were taken from a severe habitat and planted in his garden, they differentiated into several recognizably distinct forms as they recovered from transplanting.

These studies by Turesson were an important factor in bringing

about the major revolution in plant taxonomy which is only now well under way, and which for the first time gives the ecologic viewpoint the consideration it deserves in that subscience. On the basis of his experimental results Turesson proposed the following classification of plants; subsequent work by other investigators has in the main verified the correctness of his views.^{118, 120, 121, 240}

Ecophenes

(Synonyms: habitat forms, epharmones, ecads, environmentally induced variations, etc.)

These are plants differing in appearance, especially in the size of vegetative parts, numbers of stems, erectness, and reproductive vigor, but belonging to essentially homogeneous genetic stock^{12*} (Fig. 91). Their distinctness is due entirely to environmental influences, for when different ecophenes are transplanted into the same habitat these differences disappear.

As an illustration of this phenomenon, the appearance of a shrubby species of *Haplopappus* was so strongly affected by soil types that for a time taxonomists considered the ecophenes as distinct species (*H. venetus* and *H. decumbens*) until transplant studies proved their identity. Similar examples could be cited in abundance.⁴²

The ecologic importance of phenotypic plasticity lies in the fact that it has a bearing on the range of habitats a species can occupy, since it tends to make the individual adaptable to more than one habitat.

Ecotypes

(Synonyms: ecologic races, physiologic races)

A species is typically composed of a mosaic of populations, each of which differs in genetically based physiologic (and sometimes morphologic) features having survival value, and is designated as an *ecotype*. Although much mortality is accidental, individuals possessing gene combinations that are more closely attuned to local peculiarities of environment have higher probabilities of survival, and in this way each variant of the environmental mosaic tends to modify the characters of all species that invade it. Opposing this trend are dissemination and pollination which tend to carry genetic



Fig. 91. Uniform heredity in varied environment: the appearance of ecophenes developed from clonal divisions of *Potentilla glandulosa* ssp. *hansenii* grown in four markedly different environments: near the sea coast at Stanford, California; in native mid-Sierran habitat at Mather, California; and on two habitats at upper timberline. (Photograph by courtesy of J. Clausen and the Carnegie Institution of Washington.)

materials back and forth across the borders of contiguous habitat types. However, hybrids between ecotypes are incompletely adapted to either habitat, consequently selection pressure tends to eliminate

them and favor homozygosity for those characters which especially fit a plant for one habitat or the other.

Not only may ecotypes be differentiated by edaphic, microclimatic, or biotic factors,²³⁹ but also wherever a species extends across several climatic zones it may evolve a distinct climatic ecotype in each.¹²⁰ In some species the populations that are encountered along a climatic gradient are restricted to special habitats in each sector, so that the species is composed of a chain of contiguous yet reasonably distinct and homogeneous population segments, which are ecotypes.¹²⁰ In other species the adaptational pattern appears to be more in the nature of a continuous gradation (an ecocline²⁴⁰) which parallels a continuous environmental gradient, so that ecotypes could be recognized only as arbitrarily defined segments. For example, black walnut (*Juglans nigra*) trees grown from nuts obtained in Minnesota are distinctly more winter-hardy than trees grown from nuts obtained in Alabama or Texas, although materials from the two extremities of the range are morphologically indistinguishable.⁷¹³

Plant taxonomists have recently begun to recognize as subspecies the geographically distinct type of species segregate, which is the most easily studied type of morphologic variation, but from the ecologist's standpoint the practice should be extended to other types of ecotypes wherever there is morphologic basis. Races not thus distinguished, such as those of black walnut, should be indicated by accompanying notes on the region and habitat when living material is collected for cultural purposes.

Since differentiation into ecotypes results from the discriminating selection offered by unlike habitats, it follows that in general the wider the ecologic range of the species the more numerous are its ecotypes. It is possible for environmental selection to produce a complete series of races that are individually sensitive to habitat variations even if they are not macroscopically distinguishable. This may well explain strongly different habitat preferences of the same species in different regions. There are other species in which wide ecologic amplitude * seems due rather to the possession of a large reservoir of alleles without specialization than to differentiation into ecotypes with narrow but complementary requirements.

Studies of ecotypes taken from widely different climatic zones in California have shown that the ecotypes of different species which

* The range of habitat variation a plant can endure is conveniently expressed as its *ecologic amplitude*.

grow in the same habitat all tend to exhibit certain adaptational characteristics in common. For example, alpine ecotypes of all species tend to be earlier than lowland types when grown on the habitat of the lowland types.¹²⁰ In some instances the adaptations of corresponding ecotypes of closely related species are so parallel that these ecotypes resemble each other more closely than they resemble other ecotypes within their respective species. The frequency with which genetic and plastic adaptations parallel each other has long been a phenomenon causing confusion of thought, and one which is still not understood.

A single ecotype may, under suitable stimulus, be represented in several habitats by many ecophenes, and for this reason the critical delineation of ecotypes within a species usually requires experimentation. Each ecotype retains at least some of its distinctive characteristics (such as flower color and shape, habit of branching, venation, and shape of leaves) when transplanted into the same environment with others (Fig. 92), although the ecophenes of one ecotype may closely resemble another ecotype of the same species. Thus the dwarfing of a lowland ecotype transplanted into an alpine habitat may render it superficially similar to another ecotype which is confined to high altitude.

Although an ecotype has a certain degree of homogeneity with respect to ecologically critical alleles, this does not exclude variation due to heterozygosity with respect to other alleles. In fact, genetic variations within ecotypes (these variations sometimes called *biotypes*) are theoretically infinite owing to recombinations of a great store of dominant, partially dominant, and recessive genes distributed among the individuals. However, in contrast to the differences among ecotypes, the variations within them appear at random, and because they have almost no survival value these variations are not correlated with environment. Also, because most terrestrial habitats embrace an infinite number of subtle variations, natural selection cannot be expected to eliminate variations below a certain limit set by environmental heterogeneity if an interbreeding population is to remain well represented in an area.

Because ecotypes are interfertile, at least through intermediaries, they are never pure. The differences among ecotypes may be no more than a matter of difference in the frequency of occurrence of certain alleles. Therefore not all members of one ecotype could be accurately classified, even if environmental modifications could be ruled out.



Fig. 92. Varied heredity in uniform environment: the appearance of three distinct ecotypes grown in the same (mid-Sierran) habitat. *Potentilla glandulosa* ssp. *typica* transplanted from coastal habitat; *P. g.* ssp. *reflexa* native of mid-Sierran habitat; *P. g.* ssp. *nevadensis*, transplanted from alpine habitat. (Photograph by courtesy of J. Clausen and the Carnegie Institution of Washington.)

Another consequence of the fact that ecotypes are normally interfertile is that in a region where the ranges of two ecotypes overlap they exchange genes freely, even though outside this region of contact the two types exist unaltered because of constant environmental selection. There is experimental evidence that such hybridization occasionally produces new ecotypes. *Spartina townsendii*, a natural

cross between *S. stricta* and *S. alterniflora*, eliminates both parents in competition and is extending its range in Europe beyond that of either.⁴⁶⁶ These are distinct species rather than ecotypes, but the instance is valid as an illustration of the potentialities of crossing. There is much evidence that the survival of new gene combinations resulting from hybridization is rarely favored except when accompanied by the creation of a new kind of environment to which they may be preadapted, such as was provided in geologic history by the development of aridity and by the recession of glaciers to leave large areas of relatively unoccupied soil, or in recent time by the many artificial habitats created by man.

A second way in which new ecotypes may originate is through the slow accumulation of numerous small gene changes which are individually unimportant. This process is not likely in large, freely interbreeding populations, as an innovation is easily lost by the overwhelming numbers of homologous alleles. However, in a small population that is not freely exchanging genes with other populations (owing to habitat discontinuity, or merely to great distance between remote extremities of the species' range) small gene changes have a fair chance of becoming prevalent.

A third manner by which new ecotypes may arise is by chromosome changes. This is indicated by the fact that, in sexual species, polyploids from the same original stock rarely exhibit the same ecologic amplitude.⁴⁷⁸

Most changes in hereditary constitution, whether due to hybridization, gene changes, or chromosome changes, probably necessitate changes in the environment because of the close adjustment between the two. Because new ecotypes originate within the area of their parental types they must of necessity tolerate that environment, but by virtue of their different ecologic amplitudes they are able to extend into new habitats. Such a preadaptation is the more likely to succeed if it originates near the margin of the parental area, especially if such a marginal position is adjacent to a habitat that is favorable to the new entity, for this allows the new ecotype to spread quickly into new territory and thus escape submergence by interbreeding with the parental stock.

The number of ecotypes normally increases when a plant is brought into cultivation. This increase seems explainable by the fact that under cultivation there is relatively little competitive selection, which in nature would promptly eliminate many innovations.

Ecotypes are the basic units of the genecologic classification, but

other categories are necessary for grouping these units into a hierarchy showing degrees of kinship and evolutionary relationships.

Ecospecies

An *ecospecies* is a classificatory unit embracing one or more ecotypes which, though freely interfertile, do not cross or at least do not produce offspring strong enough to survive. The taxonomic species, defined for practical reasons on morphology, frequently cannot be made to correspond with the ecospecies defined on experimental tests of fertility, for sometimes two ecospecies must bear the same taxonomic designation simply because there are no useful morphologic criteria for separation. Also the role of taxonomy seems better served by recognizing as distinct species two population complexes that are geographically isolated and well differentiated, even though they may be completely interfertile.

Coenospecies

Coenospecies, the highest entities of the genecologic system, correspond to the taxonomist's section of a genus, or to all the members of a small genus. Relationships between coenospecies are so remote that genes can seldom be exchanged among them, but on rare occasions they may cross and produce either a sterile hybrid or a fertile hybrid on the level of a new species. Complex coenospecies are represented by a number of ecospecies, but at the other extreme a coenospecies may be represented by a single ecotype.

A concrete example of the application of genecology to a group of plants is provided by studies of *Potentilla* (Table 14).

This summary brings out the point of view adopted by certain well-qualified workers that morphologically indistinguishable ecotypes should not be given Latinized names but should be designated by descriptive terms and symbols. Also it is generally agreed that the genecologic terminology should never be applied to specific groups of plants until their genetic status has been determined experimentally. Until this is done the homologous taxonomic terms (subspecies, species, and section) should be applied tentatively with the understanding that experimentation will provide the final answer and may necessitate revision of any taxonomic scheme based on morphology alone.

Table 14

Taxonomic and genecologic analysis of part of one section of *Potentilla*. Five ecotypes of *P. glandulosa* span the environmental mosaic (without occupying all components of it) from the Pacific coast of central California across two mountain ranges, giving the species a very wide ecologic amplitude.¹²⁰ *Achillea* contains eleven ecotypes across the same transect.¹²¹

Coenospecies	Ecospecies	Subspecies	Segment of Environmental Mosaic	Ecotypes
<i>Potentilla</i> , Section <i>Drymocallis</i>	<i>glandulosa</i>	<i>nevadensis</i>	Alpine and upper forest belts (1,600–3,500 meters)	Alpine
		<i>hanseni</i>	Mid-altitude meadows of Sierra Nevada	All one
		<i>reflexa</i>	Well-drained slopes of Sierra Nevada (250–2,200 meters)	All one
		<i>typica</i>	Coast Range	All one
	<i>fissa</i>		Not analyzed genecologically	
	<i>arguta</i>			

Ecologic Significance of Intraspecific Variations⁶⁴⁵

Ecology, both theoretical and applied, must frequently take genetic variability into consideration in order to explain natural phenomena as well as to avoid error in experimental work.

As indicated above, a taxonomic species may consist of one to many ecotypes. It may have only one ecotype yet occupy wide geographic area if its special habitat (e.g., shallow ponds) is widely distributed. But in general, genetic variability varies directly with extent of range.

Species with many ecotypes can fit into a wide range of habitats, whereas genetically impoverished species are commonly adapted to a particular combination of environmental factors and hence have very limited ecologic amplitude. The same variation with respect to ad-

justment and tolerance extends to ecotypes, for, when plants with identical heredity are grown in different habitats, some ecotypes show little or no ability to succeed in more than one habitat, whereas others are able to tolerate wide variations in environment, even though they exhibit marked differences in appearance.^{120, 444} Genetic constitution that allows for plasticity of structure and function of the individual probably has more survival value than variability due to multiple alleles, for successive changes in environment can more easily eliminate all of the latter.

The value of a species as an indicator of particular environmental conditions is highly dependent on its degree of ecotypic specialization, for the ecotype, rather than the species, is the fundamental ecologic unit. It follows that an experimenter should file pressed specimens (*vouchers*) as an aid in settling any subsequent questions that may arise about the ecotype which was studied.

The degree of ecologic amplitude has an important bearing on the possibilities of natural or artificial extensions of species ranges. When a plant is moved from one region to another, or its original habitat undergoes change, its physiologic processes must act at a new pace dictated by the new factor intensities. Survival depends on the degree of environmental change in terms of the degree to which the plant's hereditary make-up enables it to accommodate to the change. Weeds appear to be groups with exceptionally broad ecologic amplitude, for, when they are freed of competition and original parasites and the natural barriers to their distribution are overcome, these plants prosper under a wide variety of environmental conditions. Thus *Bromus tectorum*, a Eurasian weed that has become established throughout the United States, appears to be represented so widely in the new continent by a single ecotype.³⁰⁶ As a rule, however, a vascular plant is less successful in any new habitat. Man has been able to extend the ranges of economic plants so widely only because he has produced new ecotypes,* adopted cultivation practices which compensate for much climatic adversity, and kept the plants free of serious competition from native vegetation.

In forest and range management, however, it is rarely feasible to provide any measure of freedom from competition or other habitat modifications, so that the genetic constitution must be more closely matched with the habitat factors than it is in cultivated plants. The result of a number of experiments warrants the conclusion that among

* It has been suggested that ecotypes produced by artificial selection be called *agroecotypes*.

trees, at least, few if any ecotypes are more successful in a region than those native to it.¹⁶⁸ Foresters have become so conscious of this fact that seed collections from different regions are labeled and kept separate, and nursery stock is distributed in accordance with this information.²⁷ Attempts have been made, especially with range plants, to gather together in a garden for comparative evaluation a wide selection of ecotypes belonging to economically important species. From the discussions above it should be evident that, theoretically at least, the conditions under which the selections are compared should match those under which they are to be grown, for environment may so condition the expression of hereditary characters as to suppress some and magnify others.^{590, 770} With cultivated plants this is not so necessary as with forest trees or range grasses which are given no protection after planting. It is significant to note that the comparative plantings of different ecotypes on one habitat gives results applicable to that habitat alone; relative behavior in other environments may differ considerably.¹²⁰

Theoretically the introduction of a species into a new locality is most likely to succeed if the greatest possible number of ecotypes is introduced simultaneously.^{612, 714} Not only does this increase the chances of finding a suitable ecotype among those already in existence, but also the possibility is increased that, by hybridization, a race especially suited to the new habitat may arise. Artificial crossing of ecotypes has shown that it is possible to produce new ecotypes which will grow well in an environment that neither of the parents could tolerate. This process of crossing and selection among ecotypes is the only manner by which plants become *acclimated* to new environments.

The existence of morphologically indistinguishable ecotypes points clearly to the absolute necessity of using either *clonal lines* or *pure lines* wherever possible in ecologic experimentation. A clone is a group of individuals propagated asexually from a single parent, so that they normally have absolutely uniform heredity. A *ramet* is one member of a clone. A pure line is the offspring of a homozygous, self-fertilized individual.

ISOLATION AND EVOLUTION⁶⁴⁵

Usually species and ecotypes are populations of individuals in which many if not most homologous genes differ; i.e., they are

heterozygous to varying degrees. Crossing within these populations results in countless recombinations of the different genes and allows favorable and neutral innovations to spread and become common characters. However, when a barrier prevents the mingling of new characters as they arise, separated populations sooner or later evolve along divergent lines owing to the independent accumulation and loss of genes within each population. Barriers having such an effect may be extrinsic (ecologic):

1. Geographic: seas, continents, unfavorable climatic areas.
2. Local: differences in habitat preferences.
3. Biologic: areas occupied by other organisms that are inimical to survival, or areas from which essential symbionts are excluded.

or intrinsic:

1. Physiologic: differences in time of pollination, etc.
2. Morphologic: differences in pollinating mechanisms, etc.
3. Cytogenetic: differences in chromosome number, etc.

Intrinsic barriers are permanent, and their establishment automatically transforms ecotypes into ecospecies, even if the morphologic differences are too small to warrant nomenclatorial recognition. Once extrinsic isolation has allowed intrinsic barriers to develop, a break-down of the extrinsic barriers may permit recently divergent ecospecies to mingle on the same habitat without crossing. Morphologically such ecospecies may be so similar that only experimental hybridization or the occurrence of bimodal frequency curves in random measurements of the mixed population may reveal their existence.¹³

Frequently species or subspecies represented by a single ecotype confined to a limited area exhibit exceptionally small ecologic amplitude when compared with others which, by means of genetic diversification, are represented in a variety of habitats. The apparent genetic impoverishment of these entities may arise by either of two courses of events.

First, a species may suffer one or more catastrophes which destroy all but a fragment of the total population. The remnants are called *relics*.^{*} Subsequent to the catastrophe the species is represented by

* The term *relic(t)* is also used in other senses in ecology. Any entity, such as a community, an individual, a species, a genus, that now occupies but a small part of an area or a habitat in which it was once more abundant may be referred to as a *relic* in that situation. Thus the term may have local as well as geographic application.

only one or at most a few ecotypes which carry but a limited number of contrasting alleles.

Second, an ecotype of narrow ecologic amplitude may result from a very limited crossing of an effective geographic barrier. The population descending from such a single introduction obviously can have no greater genetic heterogeneity than that possessed by the individuals that immigrated. Here specialization would not be the result of environmental selection as is true of most ecotypes, and the terms *geoecotype*,²³⁹ and *insular species*⁶⁴⁴ have been proposed for these.

It should be clear that both the above kinds of genetically impoverished entities occupy restricted areas. Thus the generalization can be drawn that the degree of genetic homogeneity is somewhat proportional to the degree of restriction in local distribution and in geographic area.

Species of small range and ecologic amplitude are in precarious positions as far as continued survival is concerned. Because of their genetic homogeneity even small changes in environment can exceed their tolerance and thus bring about extinction. On the other hand, if environment remains favorable they may persist and come to possess variability through the accumulation of mutations. Also it is theoretically possible that favorable environmental changes may come about that would allow isolated colonies to reunite and share variability acquired during the period of isolation or would allow hybridization to produce new combinations.

Free interbreeding is more effective in dispersing genes uniformly through small populations than through large, for in the latter mutations are more numerous on account of the laws of chance, yet distance alone retards gene flow. This phenomenon is added to ecotypic differentiation in bringing about a positive correlation between amount of variability and size of a species' range.

Isolated populations have unique opportunities for evolution, for new genes can easily become fixed in the absence of continual dilution. However, this is not necessarily advantageous, for neutral or even detrimental characters can become fixed just as easily. Evolutionary divergence of this nature has been called *drift* in contrast to the divergence that results from the accumulation of adaptive characters. Thus it can be seen that two subspecies may occupy different habitats that are ecologically identical even though discontinuous, and then the subspecies must be considered as still belonging to the same ecotype.

Earlier it was pointed out that adaptational variation could be discontinuous (ecotypes) or continuous (ecoclines). Nonadaptive variation also may be discontinuous, as when an island population develops morphologic distinctiveness through drift, and the term *topotype* has been suggested. If it is continuous, as illustrated by the progressive increase in ratio of scape to spike length in *Plantago maritima* from west to east across North America to Europe, the term *topoclone* is appropriate.

IN CONCLUSION

The fact that environment shapes the course of evolution was recognized with the acceptance of Darwin's work, but intensive experimentation on the problem was delayed more than half a century until developments in the field of genetics made it possible. Only within the past quarter century has it been established that the taxonomic species is not a single ecologic unit, and this has been the second major contribution of autecologic study to science. The implications of this still-unfolding concept are so important, and their appreciation so recent, that the consequences are still not fully taken into account in thinking and research.



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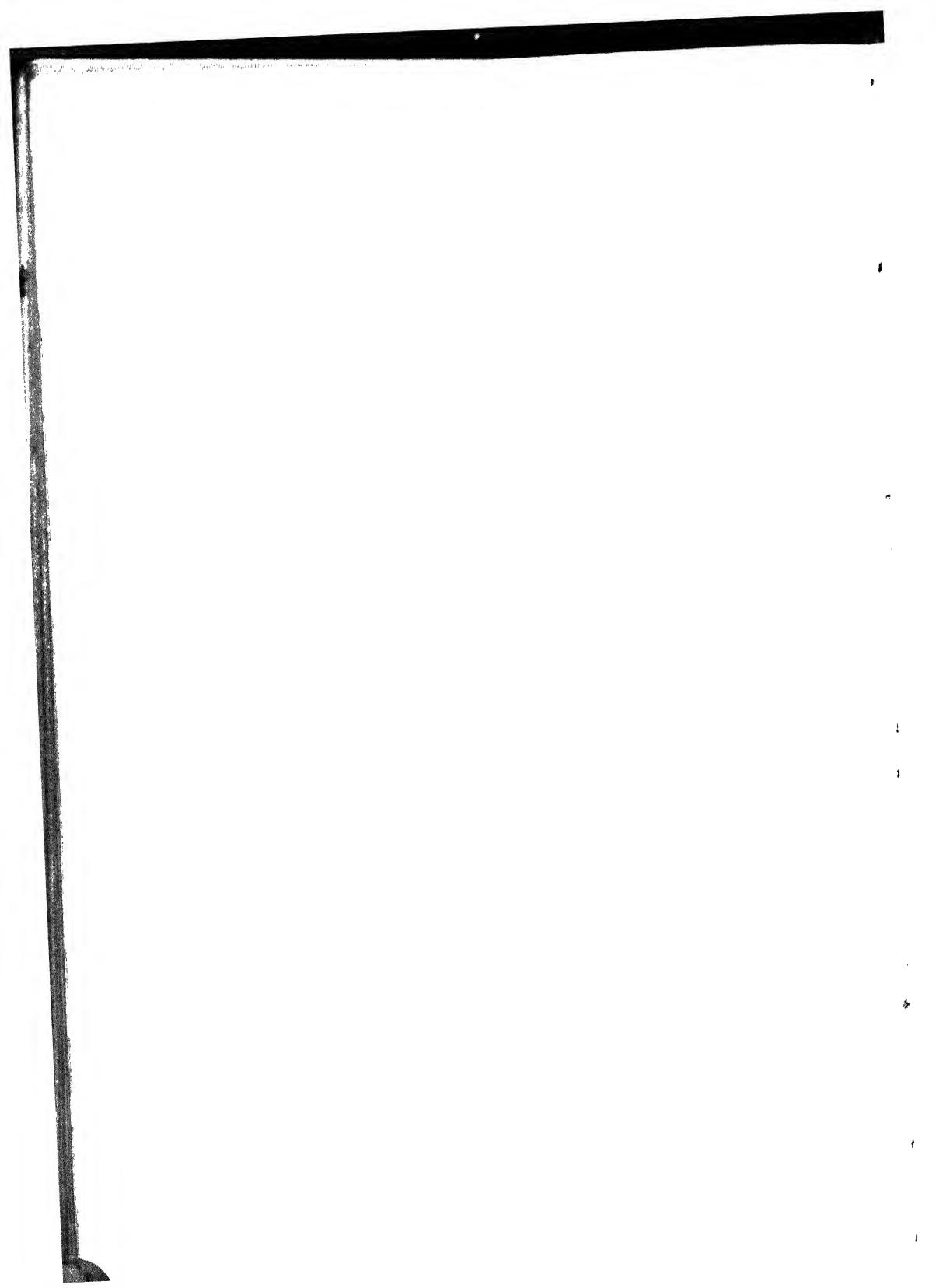
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